

THE UNIVERSITY OF KANSAS SCIENCE BULLETIN

VOL. XLI]

DECEMBER 23, 1960

[No. 9

A Survey of the Periotic Labyrinth in Some Representative Recent Reptiles

BY

IRWIN L. BAIRD

ABSTRACT: The periotic adnexa of the saccule and cochlear duct are described in some detail in fourteen reptilian families represented by a total of thirty species; brief accounts of parts of the otic labyrinth and otic capsule are included for those forms in which such descriptions seem appropriate. Modifications of the nomenclature applied to the reptilian periotic labyrinth are suggested, and certain new and hitherto-obscure periotic structures are described and named. Some suggestions concerning the evolution, the phylogenetic significance and the manner of function of the periotic labyrinth in reptiles are made and discussed.

TABLE OF CONTENTS

	PAGE
INTRODUCTION	892
MATERIALS AND METHODS	892
STRUCTURE OF THE INTERNAL EAR IN REPTILES	895
THE SACCCULO-COCHLEAR PORTION OF THE PERIOTIC LABYRINTH	
Rhynchocephalia	
Sphenodontidae	900
Squamata—Lacertilia	
Iguanidae	902
Eublepharidae	906
Sphaerodactylidae	909
Gekkonidae	911
Teiidae	915
Scincidae	917
Lacertidae	919
Anguidae	921
Varanidae	923
Squamata—Ophidia	
Colubridae	926
Chelonia	930
Crocodylia	934
DISCUSSION	938
LITERATURE CITED	963
KEY TO ABBREVIATIONS	966

INTRODUCTION

The internal ear of reptiles has been subjected to considerable morphological study, and some reports of functional investigations appear in the literature; there has been, however, relatively little attention paid to the periotic labyrinth in these animals. Retzius (1884) in his classic work, summarizes the earlier literature and considers the parts of the otic labyrinth in detail, but he tends to neglect periotic structures both in figures and in text. Some attention has been accorded the system by de Burlet (1929, 1934), and brief references to it are found in papers devoted to the cranial or auditory anatomy of specific forms or groups. There has been, however, no comprehensive survey or interpretation of the periotic labyrinth in the Class Reptilia.

This investigation was undertaken in the hope of accomplishing at least three results: (1) to provide detailed descriptions of the periotic labyrinths of a number of representatives of each of the major taxonomic assemblages of living reptiles; (2) to augment the fund of information bearing upon the evolution of the vertebrate ear; and (3) to ascertain whether or not reptilian phylogeny is reflected by the structure of the inner ear in general, and the periotic labyrinth in particular. It was additionally hoped that the study might contribute something toward a better understanding of reptilian auditory function.

I am indebted to Dr. A. S. Romer for suggesting this investigation, and for his patience, suggestions and criticisms during its course. The late Dr. G. B. Wislocki, Dr. E. E. Williams and Mr. David Hamilton have also contributed to this effort by making available to me certain materials without which the study would have been less complete, and Miss Diane Allen has given valuable assistance in the preparation of the illustrations.

MATERIALS AND METHODS

This investigation was begun using serial sections of reptilian embryos from the Harvard Embryological Collection, Department of Anatomy, Harvard University. This material proved to be limited with respect to the selection of species available, and the number of late embryos representing each species; attention was, therefore, directed toward adult specimens, the findings from embryological material being utilized only in those forms for which adult representatives were not available. The forms used are listed below. Species designated "HEC" were studied from material in

the Harvard collection; all others were represented by two or more serially-sectioned heads of adult animals.

Order Chelonia

Family Chelydridae

Chelydra serpentina

Family Testudinidae

Chrysemys marginata (HEC)

Chrysemys picta bellii

Pseudemys scripta elegans

Order Rhynchocephalia

Family Sphenodontidae

Sphenodon punctatum (HEC)

Order Squamata

Suborder Lacertilia

Family Iguanidae

Anolis carolinensis

Crotaphytus collaris baileyi

Sceloporus undulatus consobrinus

Uta stansburiana stansburiana

Phrynosoma cornutum

Phrynosoma douglassii brevirostre

Family Eublepharidae

Coleonyx variegatus

Family Sphaerodactylidae

Sphaerodactylus macrolepsis

Family Gekkonidae

Hemidactylus mabouia

Aristelliger praesignis

Family Teiidae

Cnemidophorus sexlineatus

Family Scincidae

Eumeces fasciatus

Eumeces obsoletus

Lygosoma weeksae (HEC)

Family Lacertidae

Lacerta muralis

Lacerta vivipara

Family Anguidae

Ophisaurus ventralis

Family Varanidae

Varanus sp.

Suborder Ophidia

Family Colubridae

*Carphophis amoena vermis**Diadophis punctatus arnyi**Lampropeltis calligaster calligaster**Thamnophis ordinatus parietalis**Thamnophis radix* (HEC)

Order Crocodilia

Family Crocodylidae

*Alligator sp.**Caiman sp.*

The primary method of approach in this investigation was the study of serially-sectioned material, supplemented by wax and/or graphic reconstructions. In the preparation of serial sections of the heads of adult animals, standard techniques for decalcification and sectioning did not prove to be satisfactory, since their application resulted either in excessive disruption of delicate parts of the otic and periotic labyrinths, or in loss of specimens due to lack of uniform decalcification and homogeneity in embedded tissue. A method was devised to overcome these difficulties, and a description of it will be published later.

In an attempt to clarify the relationship between the periotic and cerebrospinal fluid compartments, several specimens were subjected to radiographic study using the method of Young (1952). Several living anesthetized turtles and lizards were studied employing a modification of a technique originated and suggested orally by Dr. G. O. Proud, Department of Hearing and Speech, University of Kansas School of Medicine. In the latter method, an appropriate volume of cerebrospinal or periotic fluid was withdrawn, and replaced with an equal volume of 0.5 percent Evans Blue dye in reptilian Ringe's solution. After an appropriate interval, the animals were sacrificed and their otic regions dissected to determine the distribution of the dye.

The embryonic development of the periotic labyrinth was studied in several forms for which a number of developmental stages were available. Broadly speaking, the development of periotic spaces and definitive periotic connective tissues is similar to that in man, as described by Streeter (1918) and Bast and Anson (1949). One difference is worthy of note; in no case did late reptilian embryos (final day of incubation in *Eumeces fasciatus*)

show complete differentiation of the periotic labyrinth. This contrasts sharply with the situation in man, in which differentiation is said to be "virtually complete—at the middle of fetal life" (Bast and Anson, 1949:114). Material which will permit more thorough study of the development of the labyrinth is now being collected.

STRUCTURE OF THE INTERNAL EAR IN REPTILES

The diverse origins of the early literature concerned with the vertebrate ear, plus differences in organization of its parts in the forms considered, have resulted in an extensive synonymy and some confusion in nomenclature. It is necessary, therefore, to define terms employed in this paper before describing the periotic systems of specific forms.

Bast and Anson (1949) follow suggestions of Streeter (1918) relative to nomenclature of the fluid compartments of the internal ear, and present a particularly lucid system of terminology applicable to the internal ear of man and most other mammals. Many of their terms may be applied accurately to the reptilian ear without modification; where possible, such application has been made. In other cases, either appropriate modifications of definitions have been made, or suitable terms applied.

In its basic organization, the internal ear in reptiles corresponds to the typical vertebrate pattern. Housed within a bony enclosure, the *otic capsule* (audi'ory capsule; osseus labyrinth), are intricate, membranous, fluid-filled channels and sacs which form two morphologically distinct systems. The innermost of these, the *otic labyrinth* (membranous labyrinth of some authors), is derived from the embryonic ectodermal otocyst and contains *otic fluid* (endolymph). The second system of channels, the *periotic labyrinth* (perilymphatic system), surrounds the otic labyrinth and contributes to its fixation within the otic capsule; it contains *periotic fluid* (perilymph).

The otic labyrinth (Fig. 1) may, arbitrarily, be divided into superior (vestibular; utricular) and inferior (saccular; auditory) divisions. The former consists of the *utricle* with its macula utriculi and macula neglecta, the anterior, posterior and lateral *otic semicircular ducts* and the three *otic ampullae*. A short *utriculosaccular duct* joins the utricle with the sacculi. The inferior division consists of three major otic compartments, the intracranial *otic sac* (endolymphatic sac), the *sacculi* with its *macula sacculi*, and the *cochlear duct* (lagena of some authors). The two compartments first named are united by the *otic duct* (endolymphatic duct); the

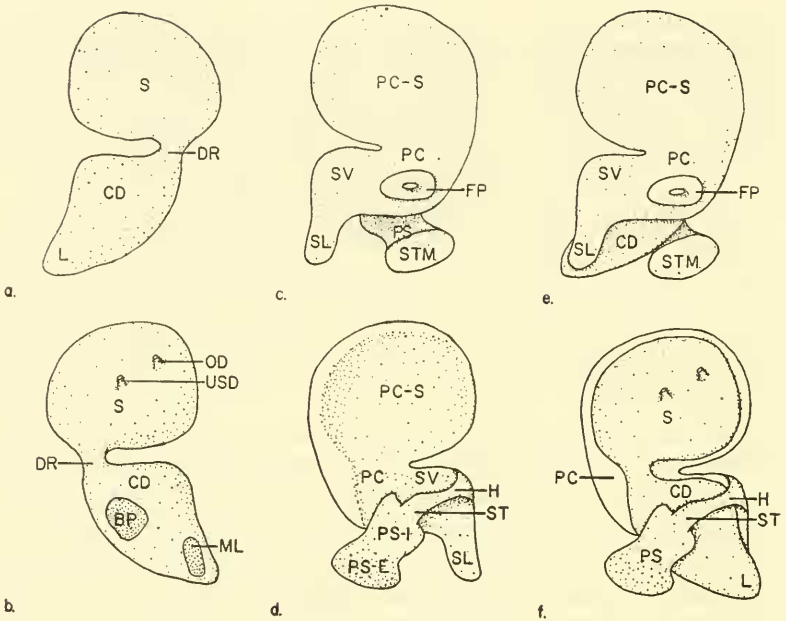


FIGURE 1. Diagram of intracapsular parts of the right otic labyrinth in a "typical" lizard; medial aspect.

sacculae communicates, at or near its posterior margin, with the cochlear duct by way of the *ductus reuniens* (sacculo-cochlear canal).

The cochlear duct is uncoiled and roughly pyramidal in shape in most reptiles. An anteroventral projection of the cochlear duct is termed the *lagena* and carries an area of sensory epithelium, the *macula lagenae*. Proximal to the lagena, part of one wall (medial in most forms) of the cochlear duct is modified to form the *basilar papilla*, a receptor homologous to at least part of the sensory cells of the organ of Corti of mammals. The basilar papilla is seated upon the *basilar membrane*, a thin sheet of connective tissue supported by the *limbus* (Knorpelschenkel or cochlear cartilage). The latter term is here used, as defined by Shute and Bellairs (1953), to include the presumed homologs of both the limbus and spiral ligament of mammals. The limbus projects, in some forms, into the cochlear duct to form a *limbic lip* (Shute and Bellairs, *ibid.*) and may support a *tectorial membrane*. The opposite wall of the cochlear duct is thin and is designated *vestibular membrane* (tegmen-*mentum vasculosum*).

The periotic labyrinth develops, and is situated in the adult, between the epithelium of the intracapsular parts of the otic labyrinth and the otic capsule; one part of the periotic labyrinth, as noted below, extends outside of the otic capsule. The labyrinth is formed of finely fibrous and mesenchyma-like tissues which may, in reptiles as in mammals, be classified on a regional basis as: (1) the *membrana propria*, which forms the intimate fibrous investment of the epithelial otic labyrinth; (2) the *internal periosteum*, which forms the fibrous lining of the otic capsule; and (3) the *periotic reticulum* (Streeter, 1918), loosely arranged or delicately organized connective tissues which extend between the two layers defined and form the spaces containing the periotic fluid.

That part of the periotic labyrinth associated with the superior division of the otic labyrinth is relatively constant in its morphology in the reptiles examined. The utricle is surrounded rather uniformly by periotic reticulum except at the points where it is joined by the semicircular ducts. Here the amount of reticulum is reduced and larger periotic lumina are present; from these areas extend the *periotic ampullae* and *periotic semicircular canals*. The former are transversed by sparse reticulum. The latter are crescentic to uncinat in cross section, confined largely to the lesser curvatures and sides of the otic semicircular ducts, and vary in size and amounts of reticulum present in their courses. Generally speaking, the lumen of the periotic semicircular canal is smallest in its middle third. Because of the uniformity, throughout the forms examined, of this part of the periotic labyrinth, it is not specifically treated in this study; rather, attention has been directed primarily toward the periotic adnexa of the inferior division of the otic labyrinth.

Three fluid compartments have classically been associated with the saccule and cochlear duct in reptiles other than archosaurs. As they are usually described, these are: (1) a large compartment situated lateral to the entire lateral walls of the saccule and cochlear duct, bounded laterally by the otic capsule and footplate of the columella auris, and designated as the perilymphatic cistern; (2) a second compartment, the perilymphatic sac, situated medial to the cochlear duct and usually possessed of diverticula which associate themselves with the cranial cavity and/or some part of the tympanic cavity; and (3) a tubular connection, called perilymphatic duct, which curves around the anterior surface of the cochlear duct to unite the two larger fluid spaces. Diverticula extending from the two larger compartments have been variously named. The material

available for this investigation indicates that more specialization may exist in this portion of the periotic labyrinth than has generally been recognized, and that the parts lend themselves to a rather uniform terminology. Retzius (1884), in some cases, suggests similar findings; he does not, however, carry these uniformly through his descriptive material.

The common periotic cavity situated internal to the footplate of the columella auris (Fig. 2) has a relatively consistent relationship to the otic labyrinth. This relationship is, in most forms, restricted to the lateral wall of the proximal (vestibular) end of the cochlear duct, the ductus reuniens and the lateral wall of the saccule adjacent to the ductus reuniens. Two extensions of this cavity can be recognized; one associates itself, primarily, with the remaining part of the lateral wall of the saccule; the other extends along one wall of the cochlear duct. The common cavity plus its saccular extension forms a compartment extremely similar to the space designated vestibule or *periotic cistern* in mammals. The latter term has commonly been applied in the internal ear of reptiles; it seems logical, therefore, to retain it for use in the restricted sense indicated.

The cochlear extension of the periotic cistern is clearly differentiated in archosaurs and more subtly so in most other reptiles; the manner in which it is delimited in each group is described below. In all forms in which it can be recognized, the cochlear extension of the periotic cistern associates itself with the vestibular membrane and extends from the common cavity toward the distal limit of the cochlear duct. This structure in reptiles appears to be at least analogous (if not homologous) to the scala vestibuli of birds and mammals, and has been recognized in archosaurs and some lizards by that term by Retzius (1884), de Burlet (1934) and others. The term *scala vestibuli* is, therefore, applied to the cochlear extension of the periotic cistern.

Application of the term perilymphatic (periotic) duct to the short narrow channel which, at the level of the lagena, connects the scala vestibuli to the periotic compartment situated adjacent to the basilar membrane, does not seem desirable. Such application falsely suggests that this structure is homologous to the mammalian periotic duct. The position, connections and form of this channel suggest that it may be more appropriately called the *helicotrema*.

The periotic compartment associated with the basilar membrane may take the form either of a sac with specialized extensions, or

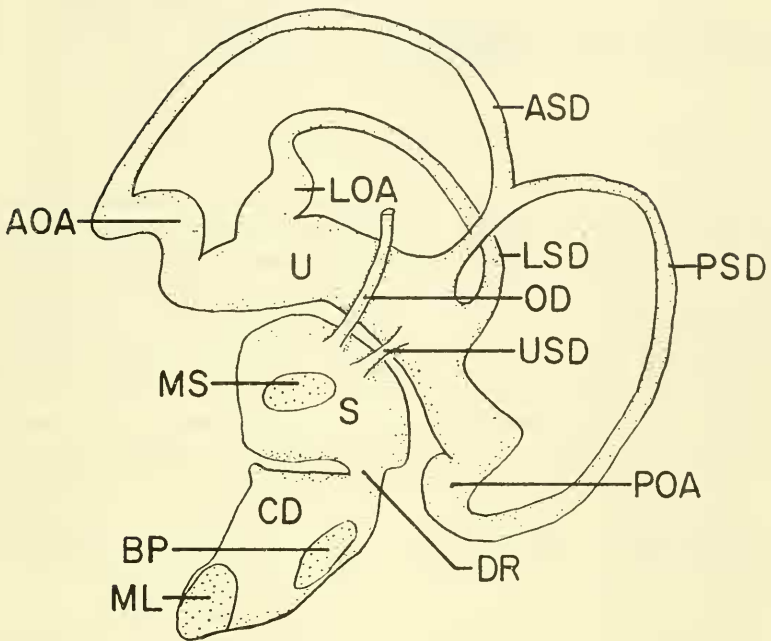


FIG. 2. Diagrams of the inferior divisions of the labyrinths in a "typical" lizard. a—Lateral aspect of left saccule and cochlear duct. c—Lateral aspect of periotic adnexus of same structures. e—Lateral aspect of combined otic and periotic parts. b, d and f—Medial views comparable to a, c and e.

one which might be loosely described as flask-shaped; in the latter case the helicotrema opens into a larger duct which extends along part of the medial cochlear wall before terminating in a sacciform enlargement. The elongate duct of the latter case is termed *scala tympani*; the irregular sac of both situations is designated *periotic sac*. Special extensions of the several parts of the labyrinth are described and named in the specific descriptive material.

The otic capsule is composed of the united *prootic* and *opisthotic* bones. *Vestibular* and *cochlear recesses* are recognized as general divisions of the central cavity of the capsule. The terms applied to the foramina of the capsule and adjacent areas are largely those employed by de Beer (1937).

THE SACCULO-COCHLEAR PORTION OF THE
PERIOTIC LABYRINTH

RHYNCHOCEPHALIA

Sphenodontidae

(Figs. 3-6; 48)

The auditory region of *Sphenodon* has received attention from an unusual number of workers. Notable contributions to the anatomy of the otic and periotic labyrinths of the species have been made by Retzius (1884), Osawa (1898) and Wyeth (1924). The relationship between the saccule and cochlear duct has been noted by these investigators (and others) to differ somewhat from the typical reptilian condition. The ductus reuniens originates from the medial wall of the saccule just posterior to its midpoint; this connection places the proximal third of the cochlear duct medial to the saccule rather than primarily inferior to that structure, as is common in most other reptiles. This difference in otic relationships, coupled with the fact that only late embryos were examined, may account for some of the complexity of the periotic cistern, noted below.

The major part of the periotic cistern is situated internal to the footplate of the columella auris, and abuts medially against the vestibular membrane of the middle third of the cochlear duct and the inferior part of the lateral wall of the saccule. The axis of this irregular cavity is oblique and corresponds roughly to the anterior margin of the saccule. An extension reaches superiorly from the medial margin of this cavity and lies in the narrow space between the saccule and related lateral wall of the cochlear duct. A narrow uncinuate extension of the cavity turns medially around the posterior margin of the cochlear duct to end blindly just short of the basilar membrane.

From the anterosuperior aspect of the major cavity, the periotic cistern extends upward about the saccule, investing the anterior half of the medial saccular wall and the greater part of the lateral saccular wall with a narrow periotic space. From the posteromedial aspect of the major cavity (that part situated between the saccule and upper third of the cochlear duct) a second extension passes superiorly, curves laterally around the posterior margin of the saccule and communicates with the lateral saccular periotic space. From the area of union of these two extensions of the major cavity of the cistern, the saccular periotic space reaches superiorly to relate itself to the posterior superior aspect of the saccule. Here it en-

larges into a cavity of considerable size. This complex association of periotic spaces, although possibly characteristic of the late embryo rather than of the adult, is considered to comprise the periotic cistern as defined above.

From the anteromedial margin of the inferior limit of the periotic cistern, a discrete, flattened, spiral, periotic channel arises. It extends forward, then turns medially around the anterior margin of the lagena to cross posteroinferiorly over the medial wall of that structure. It terminates by hooking laterally around the posterior lagena margin and narrowing to form a pointed blind ending. The course of this channel is adjacent to the entire macula lagenae, which appears to constitute its only significant relationship. Similar diverticula of the periotic cistern or scala vestibuli, although not usually as large and clearly defined as that in *Sphenodon* are present in other reptiles. Lagena extensions or diverticula of the periotic labyrinth are mentioned in the literature, but no specific name appears to have been assigned to them. The term *scala lagenae* is, therefore, suggested as being appropriate for the designation of periotic diverticula which relate themselves to the lagena, and will be used in that sense.

Immediately superior to the origin of the scala lagenae is a narrow anterior extension of the periotic cistern, which associates itself with that portion of the vestibular membrane immediately proximal (superior) to the lagena. This extension is probably homologous to the anterior part of the scala vestibuli of other reptiles, but is not considered to be clearly enough delimited to merit that name in *Sphenodon*. From the superior margin of this extension of the periotic cistern, the helicotrema originates and hooks superomedially to pass above the lagena, then posteroinferiorly to join the superior margin of an anterior extension of the periotic sac. This extension of the sac is probably homologous to the scala tympani of other reptiles, but, like the cisternal extension, it is not clearly demarcated from its parent periotic space. The helicotrema is large in *Sphenodon*, and is not as extensively surrounded by bone as it is in some other reptiles.

The periotic sac bears complex relationships to the otic capsule and cranial cavity. The anterior third of the sac is entirely intracapsular; it rests laterally against the medial wall of the cochlear duct, and is bounded medially by the medial wall of the otic capsule.

The middle third of the sac, situated directly opposite the footplate of the columella auris and related part of the periotic cistern,

is both intracapsular and intracranial. Laterally, this part of the sac contacts the relatively small basilar membrane, limbus and adjacent medial wall of the cochlear duct. Medially, it exits from the otic capsule via the large periotic (perilymphatic) foramen to enter the cranial cavity superior to, and within, the anterior part of the metotic fissure. The sac is large here, fills the greater part of the metotic fissure, and overlaps its margins to become associated with the adjacent cranial wall and floor. The walls of the sac (continuous with the intracapsular periosteum) appear to blend with the intracranial periosteum. I can detect no communication with the cerebrospinal fluid compartment (subarachnoid space of Wyeth, 1924) in this area. On the contrary, the dura mater appears to be reflected over the superomedial aspect of the periotic sac, supplementing its wall and effectively blocking any subdural communication.

The posterior third of the periotic sac is extracranial. It achieves this position by exiting through the vagus (jugular) foramen, situated toward the posterior limit of the metotic fissure, in company with cranial nerves IX, X and XI, and (according to Wyeth, 1924) the posterior cephalic vein. The blindly ending inferolateral extremity of the periotic sac approaches the wall of the pharynx, but remains separated from it by connective tissue and some of the pharyngeal musculature. I can detect no communication with interstitial spaces in this area.

SQUAMATA

Suborder LACERTILIA

Iguanidae

(Figs. 7-14)

In iguanid lizards examined, the saccule and cochlear duct are similar in size and separated along their adjacent surfaces only by a narrow condensation of the periotic reticulum. The saccule is obliquely placed within the vestibular recess; its inferolateral margin slightly overhangs the superolateral margin of the cochlear duct, and is directed toward the superior margin of the fenestra vestibuli. The ductus reuniens leaves the saccule at its postero-inferior margin and immediately joins the posterosuperior angle of the cochlear duct. The latter has the form of a blunted, laterally compressed pyramid, the base of which is directed anteromedially and includes the relatively large lagena.

In the cochlear recess, where it is impinged upon by the foot-

plate of the columella auris, the periotic cistern is laterally compressed and of small capacity. As it extends upward from this area to enter the vestibular recess, it abruptly enlarges to occupy a considerable part of that cavity. The cistern is largest in the area where it abuts against the superolateral surface of the saccule; anteriorly and posteriorly, it extends medially to invest the anterior and posterior walls of that structure.

A scala lagenae is present in all forms of this group examined. The scala appears as an inferiorly-projecting channel which originates from the anteroinferior margin of the periotic cistern (or scala vestibuli) at the level of, or anterior to, the anterior part of the footplate of the columella auris. Considerable variation in the size and form of the scala is present in the family, and this appears to be correlated with the degree of development of the macula lagenae and basilar papilla. For example, in *Anolis*, where the macula lagenae is small and the basilar papilla relatively large, the scala lagenae appears as no more than a minor projection of the periotic cistern; in *Crotaphytus*, where the macula lagenae is large and the basilar papilla is relatively small, the scala is a strong hooked channel which covers considerable portions of the lateral and posterior walls of the lagena. Other genera examined show conditions ranging between these extremes. An analysis of the scala and macula lagenae as they are correlated with degrees of development of other saccular and cochlear receptors is indicated, but is beyond the scope of this paper.

The scala vestibuli originates from the anterior margin of the periotic cistern just anterior to the footplate of the columella, and courses anteriorly along the vestibular wall of the cochlear duct to terminate in a narrow helicotrema. In *Crotaphytus*, *Sceloporus* and *Uta*, the scala vestibuli is short and poorly delimited from the overlying saccular part of the periotic cistern. Such limitation as is present appears to be accomplished by a slight, medially projecting ridge of bone along the anterolateral part of the superior margin of the cochlear recess. In *Anolis* and *Phrynosoma*, in which the scala is relatively longer, the separation of the channel is distinct. This is accomplished by means of a lamina of organized periotic connective tissue, which attaches laterally to the ridge along the anterolateral part of the superior margin of the cochlear recess, and medially to the periotic reticulum separating the adjacent surfaces of the saccule and cochlear duct. In *Anolis*, the ridge and membrane have their posterior limits slightly anterior and superior to the fenestra ovalis (vestibuli); in *Phrynosoma* the posterior

margin lies superior to the anterior part of the fenestra ovalis (vestibuli). I have been unable to find reference to this periotic membrane in the literature, although it is shown by de Burlet (1934) in a section from the ear of *Gecko*. It appears to serve primarily as a superior wall for the scala vestibuli, but in other families (described below) the membrane gives the impression of serving as a suspensory structure supporting the inferolateral margin of the sacculle. I have called the membrane the *cisternal septum*, and for convenience, shall apply the term here.

From the anterior limit of the scala vestibuli, the helicotrema turns medially around the anterior limit of the cochlear duct and lagena, and is separated from those structures by a heavy layer of periotic reticulum. In all forms examined, the helicotrema is housed in a furrow (recess of the perilymphatic duct of Oelrich, 1956) in the anterior wall of the cochlear recess. This furrow, as indicated by the above investigator, may extend along both medial and lateral walls of the cochlear recess, where it houses parts of the scala tympani and scala vestibuli. My material indicates that the depth of the furrow may vary considerably where it is related to the scalae, and indication of its presence on the external surfaces of the otic capsule may be obscured by the thickness of the bone it traverses.

Medial to the cochlear duct, anterior to the limbus, the helicotrema joins the slightly larger scala tympani. The latter courses posteriorly, inclining inferiorly in *Phrynosoma*, maintaining a practically horizontal course in *Anolis*, and inclining superiorly in the other genera examined. Medially, the scala tympani is housed in an extension of the furrow containing the helicotrema. Laterally, it is related to the limbus and cochlear rami of the posterior division of the auditory nerve. The medial relationships of the scala tympani are more intimate in *Anolis* and *Phrynosoma* than in representatives of the other genera; in the latter, a strip of loose periotic reticulum intervenes between the scala and the more medial structures. In *Anolis* and *Phrynosoma*, furthermore, the terminal part of the scala tympani is in direct contact with the basilar membrane underlying the anterior part of the basilar papilla; this situation does not obtain in other representatives of this family.

The scala tympani terminates by entering the anterosuperior aspect of the periotic sac, the intracapsular part of which is small and in immediate contact with the basilar membrane. Postero-inferiorly, the sac exits from the otic capsule, narrowing slightly

as it traverses the periotic (perilymphatic) foramen, then expands within the recessus scalae tympani. The extracapsular part of the periotic sac is large in *Phrynosoma*, *Sceloporus* and *Uta*, and relatively smaller in *Anolis* and *Crotaphytus*.

Immediately inferior to the periotic foramen, the extracapsular part of the periotic sac is related medially to the dura mater by way of the medial aperture of the recessus scalae tympani, and to the glossopharyngeal nerve, which traverses that aperture. As in other forms, I can detect no free communication between the periotic sac and the cerebrospinal fluid compartment. The dura mater appears, in my material, to form a continuous lamina over the medial extension of the periotic sac, and to clothe the glossopharyngeal nerve in its relationship to the sac. Furthermore, in *Crotaphytus*, injections of 0.5% Evans Blue into the periotic sac filled the periotic labyrinth but did not appear in the cerebrospinal fluid, and conversely, injections of the dye into the cerebrospinal fluid did not appear in the periotic labyrinth. Radiographic examinations (method of Young, 1952) also indicate that the only opening of the periotic sac is that which traverses the periotic foramen. This experimental evidence appears to support microscopic observations and indicates that any communication here between the periotic and cerebrospinal fluids is, at best, by way of a selectively permeable membrane.

From the level of the periotic foramen and medial aperture of the recessus scalae tympani, the extracapsular part of the periotic sac sweeps posteriorly and laterally to occupy part of the cavity termed by Oelrich (1956), in the related genus *Ctenosaura*, the *occipital recess*.* The external wall of this part of the sac is fused with the mucosa of the tympanic cavity to form the secondary tympanic membrane. This membrane varies considerably in its relative and absolute size within the family. It is attached to the crista interfenestralis and crista tuberalis along those surfaces which face into the recess, and, except in *Anolis*, rather close to their free margins. In *Crotaphytus*, the secondary tympanic membrane is large, looks anterolaterally into the tympanic cavity and curves posterosuperiorly from the level of the anterior margin of the apertura medialis recessus scalae tympani. *Sceloporus* and *Uta* show a rather similar situation. In *Anolis* and *Phrynosoma*, the secondary tympanic membrane faces inferolaterally and postero-

* This term appears to be synonymous with the term *recessus scalae tympani* as used by Romer (1956) and others; see discussion.

laterally, respectively, and does not extend significantly posterior to the level of the medial aperture of the recessus scalae tympani.

Eublepharidae

(Figs. 15-16)

In *Coleonyx*, the saccule is distinctly smaller than the cochlear duct and separated from that structure except anteriorly where it slightly overhangs the superolateral margin of the duct. Attached to the central part of the lateral saccular wall is a relatively small, densely organized mass of connective tissue; this is situated opposite the saccular macula and seems to represent an elaboration of the membrana propria. The mass has no other attachments and appears to be maintained in position solely by the surrounding, thin, lateral wall of the saccule. At its posterior limit, the saccule opens freely into the ductus reuniens, which descends to open into the posterior superior angle of the cochlear duct. The latter structure is large, carries a posteriorly-elongated basilar papilla, and has associated with its medial wall a large limbus with a well-developed limbic lip (see Shute and Bellairs, 1953). Otherwise, its structure is similar to that in most other lizards.

The major part of the periotic cistern abuts against the lateral walls of the posterior halves of the saccule and cochlear duct. The cochlear part of the cistern is somewhat narrower than the saccular part, and is in contact laterally with the antero-posteriorly elongated footplate of the columella auris. The saccular part of the cistern extends anteriorly and posteriorly to relate itself to the entire lateral, and the anterior and posterior surfaces of the saccule.

The scala vestibuli forms an anterior extension of the cochlear part of the periotic cistern, and is related to the anterior half of the vestibular membrane. The scala has its posterior limit at the level of the anterior margin of the columellar footplate, above which a distinct medially-projecting ridge of bone arises and extends forward to mark the superolateral margin of the anterior part of the cochlear recess. This ridge, more prominent anteriorly, forms the lateral part of the roof of the scala vestibuli and gives attachment to a cisternal septum, which forms the medial part of the roof. Posteriorly, the septum is formed by a lamina extending solely from the membrana propria of the inferior margin of the saccule; anteriorly, the septum is heavier, and is attached medially to both the membrana propria and the periotic reticulum inferomedial to the saccule.

A narrow periotic diverticulum arises from the superomedial aspect of the scala vestibuli near its posterior limit, and extends superomedially (and slightly anteriorly) between the opposing surfaces of the saccule and cochlear duct. Medial to the saccule, the diverticulum expands into a periotic chamber related to the inferomedial wall of the saccule. This chamber extends primarily rostrally, surrounded except along its saccular surface by periotic reticulum, and is related to the base of the saccular macula. The chamber appears to end blindly just short of the anterior limit of the saccule, but the material available does not allow me to be positive on this point. Although this diverticulum is indirectly related to the superior wall of the cochlear duct and the lateral wall of the utricle, it is most intimately related to the saccule and the base of the saccular macula. I can find no reference to this channel in the literature, and have called it the *scala sacculi*.

A small but distinct scala lagenae is present in *Coleonyx*. Arising from the anteroinferior margin of the scala vestibuli, it reaches along the lateral wall of the lagena to its anterior limit, and extends inferiorly to hook medially below the lagenar floor. Superior to the scala lagenae, the scala vestibuli communicates with the helicotrema. This is, laterally, housed in a deep groove in the lateral wall of the cochlear recess and separated from the cochlear duct by a dense layer of periotic reticulum. As the helicotrema follows its short rostral course, the groove deepens and, at the anterior limit of the cochlear duct, continues into a bony canal in the anterior wall of the cochlear recess. Within this canal, the helicotrema hooks medially, inferiorly and posteriorly. Following this diagonal curved descent, it re-enters the cochlear recess where it lies in a deep groove in the medial wall of the recess, immediately inferior to the foramen transmitting the posterior ramus of the auditory nerve. The helicotrema passes medial to the lagenar ramuli of that nerve, and communicates with the scala tympani at the level of the anterior extremity of the limbus. The latter channel is short; it courses posteriorly, medial to the anterior extremities of the limbus, basilar membrane and basilar papilla, and inferior to the anterior part of the cochlear ganglion. It terminates by entering the periotic sac at the level of the anterior margin of the periotic foramen, opposite the anterior margin of the footplate of the columella auris.

The periotic sac is relatively small in *Coleonyx*. Laterally, it abuts against the central part of the basilar membrane; inferiorly, it extends freely into the recessus scalae tympani by way of a large

periotic foramen. The intracapsular part of the sac is extended posteriorly and superiorly in relation to the posterior part of the basilar membrane and papilla by means of a diverticulum. This channel, described by Shute and Bellairs (1953) as "a diverticulum from the perilymphatic sac," occupies a groove in the lateral surface of the limbus and, tapering throughout its course, extends to end blindly at the posterior limit of the basilar membrane and papilla. The posterior limits of all three structures lie opposite the posterior margin of the footplate of the columella auris. Since specialized periotic diverticula are relatively common in the ears of reptiles, it would seem desirable to recognize this channel by a more specific term than has been suggested by those who originally described it; I suggest, therefore, that the term *accessory scala tympani* be used to designate diverticula of this sort.

The extracapsular part of the periotic sac is, anteriorly, poorly delimited from the intracapsular part. This is the result, primarily, of differences in the attachments of the secondary tympanic membrane from those noted in iguanid lizards. Anterolaterally, the membrane attaches to the otic capsule along the external margin of the periotic foramen; posterior to the limit of the foramen, the lateral attachment is to a slight ridge on the inferior surface of the otic capsule. The entire medial attachment is to the basis cranii along a line immediately inferior to the medial aperture of the recessus scalae tympani. These attachments place the secondary tympanic membrane at the depths of the recessus scalae tympani rather than toward its lateral margins, and cause the membrane to face inferiorly into the recess rather than laterally or inferolaterally into the tympanic cavity proper. Thus, in the region of the periotic foramen, the periotic sac is triangular in cross section; superolaterally it contacts the basilar membrane; medially it contacts the meninges via the medial aperture of the recessus scalae tympani; and inferiorly it enters into the formation of the secondary tympanic membrane. Posterior to the periotic foramen, the sac extends posteriorly for a short distance, inferomedial to the otic capsule. In this area it is traversed by the ninth cranial nerve, which exits from the cranial cavity through a foramen situated immediately posterior to the medial aperture of the recessus scalae tympani. As in other forms, no communication between the periotic sac and cerebrospinal fluid compartment could be detected.

Sphaerodactylidae

The structures of the internal ear in *Sphaerodactylus* show remarkable shortening of their antero-posterior axes, accompanied by an apparent increase in their vertical dimensions. This is marked in the saccule and cochlear duct, both of which give the impression of being antero-posteriorly compressed and vertically attenuated. The saccule is additionally modified in that part of its lateral wall, is drawn laterally and, except at its anterior and posterior extremities, firmly attached to the lateral wall of the vestibular recess. The attachment is made by (apparently) an elaboration of the membrana propria in the area corresponding to the position of the connective tissue mass noted in *Coleonyx*. This elaboration extends over, and greatly thickens, the free superolateral wall of the saccule. Thus, only the inferolateral part of the lateral saccular wall is thin, since the inferomedial wall rests upon dense periotic reticulum occupying the narrow space between the cochlear duct and overlapping saccule, and, more dorsally, between the saccule and utricle.

The ductus reuniens is small, and joins the saccule and cochlear duct at their posterior margins. The cochlear duct is smaller than the saccule and neither the limbus nor the basilar papilla shows elongation. The round footplate of the columella auris is situated lateral to the duct, directly opposite and slightly anterior to the basilar papilla.

The major cavity of the periotic cistern lies adjacent to the posterior halves of the vestibular membrane and inferolateral wall of the saccule. In this area, it is rather distinctly divided into saccular and cochlear parts by a ridge of bone which projects superomedially from the lateral superior margin of the cochlear recess; the division is least marked immediately superior to the footplate, where the ridge is lowest. The saccular part of the cistern sweeps superiorly, anterior and posterior to the attached part of the lateral saccular wall, and extends above the area of attachment adjacent to the thick, free, superolateral wall of the saccule. Thus, the saccular part of the periotic cistern forms a roughly circular cavity, which surrounds an axis formed by the saccule and its lateral attachment and communicates ventrally with the cochlear part of the cistern.

The scala vestibuli is short, corresponding to the shortness of the cochlear duct; it originates from the cochlear part of the periotic

cistern just rostral to the anterior limit of the columellar footplate. At this level, the ridge along the superolateral margin of the cochlear recess inclines medially, forming the lateral part of the roof of the scala, and gives attachment to a cisternal septum, which extends to the periotic tissue inferomedial to the saccule and forms the medial part of the scalar roof. The scala vestibuli contacts virtually the entire lateral wall of the cochlear duct and lagena, hence, no discrete scala lagenae can be identified. No scala sacculi is present.

Anteriorly, the scala vestibuli terminates abruptly and communicates with the helicotrema, which, at the level of the anterior margin of the cochlear duct, arises as a narrow channel from the superior part of the scala. The helicotrema does not perceptibly groove the wall of the cochlear recess, but passes through dense periotic reticulum and, almost immediately, enters a bony canal in the anterior wall of the cochlear recess. In this canal it hooks medially and descends, then, still in the canal, turns posteriorly along the medial wall of the cochlear recess. The helicotrema terminates medially just anterior to the level of the anterior margin of the columellar footplate, where the bony canal opens into the cochlear recess; here the helicotrema communicates with the scala tympani. The latter is situated ventral to the cochlear ganglion and lies in a groove on the medial surface of the limbus. These relationships are maintained while, expanding in size, the scala traverses a short course posteriorly. At the level of the posterior part of the footplate of the columella, the scala tympani contacts laterally the anterior part of the small basilar membrane. Immediately posterior to this, it terminates in the anterosuperior part of the periotic sac.

The periotic sac is remarkably compact in *Sphaerodactylus*. It is situated posterior to the level of the posterior margin of the footplate of the columella, and contacts no more than half of the basilar membrane. Inferomedially it passes freely through the periotic foramen and occupies the deeper half of a small and poorly-defined recessus scalae tympani. Intra- and extracapsular parts of the sac can be only arbitrarily defined, since the sac is restricted to the small area inferomedial to the periotic foramen. Viewed in transverse section, the sac is triangular; superolaterally it contacts the posterior part of the basilar membrane and adjacent limbus, medially it rests against the dura mater at the medial aperture of the recess, and inferolaterally it fuses with the mucous membrane of the tympanic cavity to form the secondary tympanic membrane. The

sac does not extend posterior to the level of the posterior margins of the periotic foramen and medial aperture of the recessus scalae tympani. No communication of the periotic sac with the cerebrospinal fluid compartment could be discerned, and no accessory scala tympani is present in *Sphaerodactylus*.

Gekkonidae

(Figs. 17-20)

In both *Aristelliger* and *Hemidactylus*, the saccule is approximately the same size as the cochlear duct, has approximately equal longitudinal and vertical measurements, and appears to be suspended obliquely in the vestibular recess between two ridges of bone. The inferior ridge is that marking the lateral superior margin of the cochlear recess; the superior ridge arches longitudinally along the vestibular roof from just lateral to the anterior ampulla to just lateral to the posterior ampulla. In *Aristelliger* the inferolateral margin of the saccule actually touches and attaches to the opposing ridge throughout its length. In *Hemidactylus*, a similar relationship is present anteriorly, but, from a short distance anterior to the footplate of the columella to a level just posterior to the mid-point of that structure, the inferolateral attachment of the saccule to the ridge is made by means of a cisternal septum. Additionally, in this form, the central part of the lateral wall of the saccule makes a strong attachment to the superolateral wall of the vestibular recess. This is accomplished by an even greater elaboration of periotic connective tissue than that seen in *Sphaerodactylus*. In the latter, the connective tissue followed the contour of the saccule; in *Hemidactylus* the mass is larger, denser and more highly organized, and gives the impression of infringing upon and reducing the size of the cavity of the saccule. In sectioning, its density produces some disruption in the tissues surrounding it, so that it is impossible to state precisely the relationships of the mass to the saccular wall.

The lateral saccular wall is free and unmodified in adult specimens of *Aristelliger*. Late embryos labelled *A. praesignis* in the Harvard Embryological Collection show a definite contact and weak attachment of the lateral saccular wall to the lateral wall of the vestibular recess, but the organization of the remaining parts of the ear suggests that a remarkable reorganization occurs in the ear postnatally, or during terminal embryonic development.

Like the saccule, the ductus reuniens in *Aristelliger* differs notably from that in *Hemidactylus*. In the latter, the duct is small, short, tubular and extends from the posteroinferior angle of the saccule

to the posterosuperior angle of the cochlear duct. In *Aristelliger*, on the other hand, the duct is antero-posteriorly wide, laterally compressed and leaves the saccule posteromedially. It makes a broad communication with the cochlear duct and is associated, medially, with the posterior extremity of the limbus.

The pyramidal cochlear ducts are basically similar in the two forms examined; differences noted do not significantly alter the organization of the associated parts of the periotic labyrinth. The basilar membrane and papilla are elongate in both forms.

Because of the extended inferolateral attachment of the saccule in these gekkonids, the part of the periotic cistern common to the saccule and cochlear duct is confined to those small portions of the vestibular and cochlear recesses which lie posterior to the level of the shaft of the columella auris. This part of the cistern contacts a small part of the lateral wall of the saccule in *Hemidactylus*; it is lateral only to the ductus reuniens and lies posterior to the saccule and cochlear duct in *Aristelliger*. The saccular part of the cistern extends anteriorly in the vestibular recess to form a large compartment, simple and superolateral to the saccule in *Aristelliger*, but encircling the saccular attachment in *Hemidactylus*, much as it does in *Sphaerodactylus*.

The scala vestibuli is related to the entire lateral wall of the cochlear duct in *Aristelliger*, and all but its hindermost extremity in *Hemidactylus*. The footplate of the columella auris, elongate in the former, confines its contact to the scala in that form; in *Hemidactylus*, the round footplate, posterior to the level of its shaft, makes minor contact with the periotic cistern, but the greater part of its area rests against the scala vestibuli.

In both forms a strong scala sacculi is present. In *Hemidactylus*, it arises from the superolateral margin of the scala vestibuli anterior to the level of the anterior margin of the footplate, extends between the opposing surfaces of the saccule and cochlear duct, then expands into a "Y-shaped" compartment, the posterior limb of which is considerably larger than the anterior. Both limbs of this compartment end blindly, and the whole lies against and closely corresponds to the shape of the base of the saccular macula. In *Aristelliger*, a more complex relationship is present. Opposite the entire extent of the footplate, the scala vestibuli extends superomedially in contact with the high lateral wall of the cochlear duct; this extension is related superolaterally to the inferomedial saccular wall, and is continuous posteriorly with the periotic cistern.

At the level of the anterior limit of the footplate, the superior margin of the cochlear duct becomes attached by periotic connective tissue to the inferomedial saccular wall near its lateral limit, leaving a part of the extension of the scala vestibuli confined above the attachment. The channel so formed extends rostrally, lying against the central part of the medial wall of the saccule for its full length, and communicates anteriorly with the saccular part of the periotic cistern in the anterior part of the vestibular recess. A second communication is made between the scala vestibuli and longitudinal part of the scala sacculi posterior to the helicotrema, opposite the anterior part of the limbus. This channel is in a position similar to the single communication noted in *Hemidactylus*. Although the scala sacculi lies at the base of the macula sacculi in *Aristelliger*, it is separated from it by rather dense periotic reticulum, not unlike that which separates it from the utricle and cochlear duct. This differs from the condition in *Coleonyx* and *Hemidactylus* in which there is intimate contact between the scala and base of the macula.

A scala lagenae is present in both forms. It constitutes no more than an inferiorly-directed triangular projection of the anterior part of the scala vestibuli in *Hemidactylus*. In *Aristelliger*, the scala is larger and extends inferiorly from the terminal part of the scala vestibuli and lateral part of the helicotrema. It relates itself not only to the lateral wall of the lagenae, but hooks beneath it in contact with its inferior and the lower part of its medial surface, and sweeps anteriorly in contact with the lower part of the anterior surface. Thus, the lagenae is virtually ensheathed by the lagenar scala in this form.

The scala vestibuli terminates in the helicotrema just posterior to the anterior limit of the cochlear duct in both forms examined. Occupying a rather shallow groove, the helicotrema hooks medially and inferiorly around the anterior wall of the cochlear recess. It is related to the anterior limit of the cochlear duct and lagenae rather closely in this course, and, in *Aristelliger*, is separated from the anterior part of the scala lagenae only by a thin layer of periotic reticulum. Medial to the cochlear duct it passes posteriorly in a canal formed by grooves in the wall of the cochlear recess and anterior part of the limbus; here it passes inferior to the posterior ramus of the auditory nerve and cochlear ganglion, and medial to its lagenar ramuli. In both forms the helicotrema terminates in the scala tympani at the level of the anterior limit of the limbic lip.

The scala tympani is short; it courses posteriorly, related laterally,

first to the limbus, then to the anterior part of the basilar membrane and papilla. It achieves the latter relationship just rostral to the level of the anterior margin of the periotic foramen, where it terminates by communicating with the periotic sac.

In *Hemidactylus*, a considerable part of the periotic sac lies anterior to the level of the rostral margin of the footplate of the columella auris. In this area, its immediate relationships are similar to those noted in *Coleonyx* and *Sphaerodactylus*; specifically, it rests against the basilar membrane superolaterally, and extends through the periotic foramen into the superomedial part of the recessus scalae tympani, where it is in contact with the dura mater medially and secondary tympanic membrane inferiorly. Opposite the anterior part of the footplate, the medial aperture of the recessus and the periotic foramen are closed, and the sac occupies an extracapsular position inferomedial to the posterior part of the otic capsule. Facing inferiorly into the recessus scalae tympani, it extends posteriorly in this position only to the level of the shaft of the columella, opposite which it is crossed medially by the ninth cranial nerve. The latter exits from the cranial cavity by way of a small foramen immediately posterior to the medial aperture of the recessus scalae tympani.

In *Aristelliger* the anterior limits of the periotic sac and foramen lie opposite the rostral extremity of the footplate of the columella. At precisely the same level, an extremely narrow vertical slit in the bony wall of the cranial cavity places the periotic sac in contact with the meninges. It is possible that this slit represents a reduced medial aperture of the recessus scalae tympani, for the relationships of the periotic foramen and sac to it are identical with those noted in other gekkonoids. For a short distance posterior to this opening, the wall of the cranial cavity is complete, and the periotic sac rests against bone medially, the basilar membrane superolaterally and the secondary tympanic membrane inferiorly. At the level of the anterior surface of the shaft of the columella auris, the periotic foramen closes and a second foramen appears in the cranial wall medial to the periotic sac. This large opening anteriorly transmits the ninth cranial nerve and allows contact of the extracapsular part of the periotic sac with the dura for a considerable distance. After traversing the foramen, the ninth nerve, superomedial to the periotic sac, courses caudally to the level of the posterior margin of the footplate, where the sac has its posterior limit. The entire secondary tympanic membrane, which faces inferiorly into the recessus scalae

tympani, is thick and heavily pigmented. In neither form does the periotic sac appear to communicate with the cerebrospinal fluid compartment.

In both forms an accessory scala tympani arises from the posterosuperior aspect of the intracapsular part of the periotic sac. It inclines posterosuperiorly, occupies a groove in the lateral surface of the limbus and laterally abuts against the posterior part of the basilar membrane. In *Hemidactylus*, the accessory scala extends from the level of the anterior part of the footplate to the level of its posterior margin; in *Aristelliger*, the accessory scala is shorter and lies opposite only the central part of the elongate footplate.

Teiidae

(Figs. 21-23)

The saccule, smaller than the cochlear duct in *Cnemidophorus*, is placed obliquely in the vestibular recess with its superior margin inclined distinctly medially. This is more marked posteriorly where the saccule forms an angle of approximately ninety degrees with the vertical posterior part of the cochlear duct. The inferomedial wall of the saccule is thickened, particularly posteriorly, by a layer of dense periotic connective tissue resembling that of the limbus. Throughout the length of the saccule, the lateral part of this layer touches and attaches to the thick superior wall of the cochlear duct, and, posteriorly, blends into the posterior part of the limbus.

Precise delimitation of the ductus reuniens is difficult because of the intimate association of the adjacent surfaces of the saccule and cochlear duct. Arising as an inferolateral extension of the posterior extremity of the saccule, it is short, duplicates the obliquity of the posterior part of the saccule, and joins the medial aspect of the posterosuperior extremity of the cochlear duct. The latter extends anteroinferiorly in the cochlear recess past the anterior limit of the saccule. Posteriorly, in the region of its association with the limbus, the vertical and transverse dimensions of the duct are considerably smaller than they are anteriorly in the region of the lagena. The basilar membrane and limbic opening housing it take the form of ovals, the long axes of which are vertical; they are situated directly opposite the footplate of the columella auris.

The periotic cistern is large and occupies approximately the lateral halves of both the vestibular and cochlear recesses. The cochlear part of the cistern is narrower than the saccular part, but is in free communication with the latter throughout its contact with the

lateral wall of the cochlear duct. The anteroinferior margin of the cistern extends inferiorly as the scala lagenae, but this structure is short and poorly demarcated from the general cavity.

The helicotrema is small and arises from the anterior margin of the periotic cistern adjacent to the anterosuperior margin of the lagena. It turns medially in a shallow groove in the anterior wall of the cochlear recess, then posteriorly along the medial wall, where the groove becomes shallower and disappears at the level of the anterior margin of the posterior acoustic foramen. The medial limb of the helicotrema is related laterally to the dense periotic reticulum of the medial lagenar wall and to lagenar ramuli of the eighth nerve. It passes inferior to the posterior acoustic foramen and terminates in the scala tympani at the level of the posterior margin of that foramen and anterior extremity of the limbus. In contact with the cochlear ganglion superiorly, the scala tympani expands inferolaterally into limbic tissue and empties into the periotic sac superior to the rostral margin of the periotic foramen.

The intracapsular part of the periotic sac forms a transversely-narrow, inferolaterally-expanded, blind ending to the scala tympani. It is short antero-posteriorly, corresponding to the erect oval shape of the basilar membrane, which it touches laterally. Bounded superiorly by limbic tissue and a laterally-directed lip on the superior margin of the periotic foramen, the sac extends medially (and slightly inferiorly) through that foramen. Directed toward the cranial cavity, the extracapsular part of the sac rests against the dura mater and, opposite the root of the glossopharyngeal nerve, bulges strongly through the medial aperture of the recessus scalae tympani toward the brain. Inferolaterally, the wall of the periotic sac enters into the formation of the secondary tympanic membrane. The latter, narrower anteriorly than posteriorly, stretches between the inferior margin of the medial aperture of the recessus scalae tympani and the lateral margin of the periotic foramen. Thus, the extracapsular part of the periotic sac is confined in the superomedial part of the recessus scalae tympani and the secondary tympanic membrane faces into the unoccupied part of the recess; the latter forms a broad shallow fossa in the inferior part of the medial wall of the tympanic cavity. The glossopharyngeal nerve traverses the medial aperture of the recessus scalae tympani, passing inferior to the central part of the periotic sac, and courses posteriorly in this fossa.

Scincidae

(Figs. 24-28)

The following description is based primarily upon the conditions found in the two species of *Eumeces* investigated. The specimen of *Lygosoma* available to me showed some disruption in the intracapsular structures, and although it appears to agree in essential features, it does not offer a firm basis for detailed analysis.

The gross form and relationships between the saccule and cochlear duct do not differ radically from the conditions described in iguanids. The saccule is, relative to the cochlear duct, larger in size than in the Iguanidae and projects laterally more markedly than in that family. The limbus, basilar membrane and basilar papilla show modification in that they are elongated anteroinferiorly in their relationship to the medial cochlear wall.

The periotic cistern has a form similar to that described in iguanid lizards except that there is less distinction between the saccular and cochlear parts. That part of the cistern impinged upon by the footplate of the columella auris appears in cross section as a triangular downward projection of the saccular portion, and is related only to the posterior part of the cochlear duct. From this region, the cistern extends superiorly and anteriorly, becomes larger, and relates itself to the saccule, except along its inferomedial surface.

Just anterior to the fenestra vestibuli, a well-defined cisternal septum extends from the periotic reticulum medial to the saccule and, apparently, from the membrana propria of the saccule itself, to a ridge marking the anterolateral part of the superior margin of the cochlear recess. This septum forms the superior wall of the scala vestibuli, which extends anteromedially and inferiorly, related to the vestibular wall of the cochlear duct. Laterally, the scala is bounded by the wall of the otic capsule. Anteriorly, the scala vestibuli gives rise to a clearly differentiated scala lagenae, which extends inferiorly to abut against the lateral and anterolateral surfaces of the lagena.

The helicotrema arises from the anterosuperior extremity of the scala vestibuli, and turns medially and inferiorly to cross the anterior limit of the cochlear duct superior to the lagena. The helicotrema is lodged in a deep furrow in the bone of the anterior wall of the cochlear recess.

The scala tympani courses posteriorly, traversing a shallow groove in the medial wall of the cochlear recess. In its course, it is related laterally and sequentially to the cochlear rami of the auditory

nerve, the cochlear ganglion and limbus, and to the limbus alone; it does not relate itself to the basilar membrane. The scala tympani terminates by entering the anterosuperior aspect of the periotic sac approximately at the level of the anterior margin of the footplate of the columella auris.

The intracapsular portion of the periotic sac lies low in the posterior part of the cochlear recess directly opposite the footplate of the columella auris. It abuts, laterally, against the posterior part of the basilar membrane and, posteroinferiorly, exits from the otic capsule by way of the periotic foramen.

The intracapsular part of the periotic sac gives rise to a vermiform channel or diverticulum, which extends anteroinferiorly, as far as the lagena, in relation to the anterior part of the basilar membrane. The channel is accommodated by a hollowing out of the limbus medial to the basilar membrane; thus, a thin layer of limbic tissue separates the channel from the medial wall of the otic capsule. A periotic channel similar to this has been noted and partially described by Retzius (1884) in *Eumeces (Plestiodon)* and in the related genera *Acontias* and *Egernia*. The author terms the channel the "scala tympani" (his quotes) and states that it may communicate with a periotic space related to the lagena. I have been unable to detect the latter communication in *Eumeces*, but have a few specimens in which disruption of structures could lead to this interpretation. The primary part of the channel, that related to the basilar membrane, does not appear to be the homolog of the accessory scala tympani of the gekkonoids; it is, however, sufficiently similar to that structure in morphology and apparent function that, by analogy, I recognize it by the same name.

The extracapsular part of the periotic sac is related, via the medial aperture of their recessus scalae tympani, to the dura mater, and as in other families, shows no communication with the cerebrospinal fluid compartment. The glossopharyngeal nerve, as noted in some specimens of *E. quinquelineatus* by Rice (1920) and de Beer (1937), relates itself to this part of the sac via a separate foramen (foramen glossopharyngei internum). The interpretation of the latter author agrees with my material, for the course of the nerve appears to be distinctly outside the confines of the cavity of the otic capsule, but does traverse an inferior extension of its medial wall. This course was noted in all specimens of both *Eumeces fasciatus* and *E. obsoletus*.

The extracapsular part of the periotic sac expands posteriorly and laterally beneath the posterior part of the otic capsule, where

it occupies the recessus scalae tympani completely. At the lateral aperture of the recess, the inferolateral wall of the periotic sac joins the tympanic mucosa to form the secondary tympanic membrane. The latter is relatively (and probably absolutely) larger in *E. fasciatus* than it is in *E. obsoletus*.

Lacertidae

Figs. 29-31

The organization of structures of the inner ear in *Lacerta* has been covered, or touched upon in part, by an unusual number of investigators (Clason, 1871; Hasse, 1873 a & b; Retzius, 1884; Gaupp, 1900; de Burel, 1934; and others) and is frequently cited as exemplary of the saurian inner ear. Of the more detailed coverages, that of Retzius is particularly complete, and my own observations on the otic labyrinth and capsule in *Lacerta muralis* and *L. vivipara* agree in practically all basic features with his in *L. viridis* and *L. ocellata*. Separate consideration of these parts is, therefore, omitted.

The periotic cistern is small and restricted almost exclusively to small parts of the lateral surfaces of the cochlear duct and saccule posterior to the level of the footplate of the columella auris. Little, if any, periotic fluid is associated with the lateral and superolateral surfaces of the greater part of the saccule, for, in adult specimens, that organ is expanded and, except at its anterior and posterior extremities, occupies the lateral two-thirds of the vestibular recess. Its lateral and superolateral surfaces are in contact with the wall of the recess, and the membrana propria is closely attached to the internal periosteum. [This differs from the conditions described by Retzius and some others. Their observations may well have been made on embryos, however, for several late embryos of *L. muralis* in the Harvard Embryological Collection show the periotic cistern extending over the lateral and superolateral surfaces of the saccule (Figs. 29-31) in the manner those investigators describe.]

From the small posteriorly-placed cistern, the scala vestibuli extends rostrally, lateral to the cochlear duct and lagena, and is impinged upon by the footplate of the columella auris. The greater part of its roof is formed by the inferior part of the expanded wall of the saccule, but anteriorly, where the saccule is somewhat smaller and shows a small periotic space along its inferolateral surface, a short cisternal septum extends from the membrana propria of the inferomedial saccular wall to the superior lateral margin of the cochlear recess and forms the scalar roof. In the same area, a space exists

between the superior surface of the lagena and the opposing surface of the saccule; through this, a scala sacculi extends superomedially from the scala vestibuli and expands into a channel in contact with the inferomedial surface of the saccule. Although it extends to communicate with periotic spaces anterior and posterior to the saccule, the scala sacculi is distinct and unobstructed only where it is related to the base of the macula sacculi; anterior and posterior to this region, it is transversed and made less distinct by loosely organized periotic reticulum. In addition to the scala sacculi, a small scala lagenae arises and extends inferiorly from the anteroinferior margin of the scala vestibuli in both species examined.

The helicotrema is relatively large at its origin from the anterior extremity of the scala vestibuli and as it grooves the anterior wall of the cochlear recess in passing medially around the anterior extremity of the lagena. Medial to the lagena, where it is housed in a deep furrow in the medial wall of the cochlear recess, the diameter of the helicotrema is reduced and remains so posteriorly to the level of the anterior extremity of the limbus. Here the helicotrema continues into the scala tympani. The latter is short, but expands rapidly as it crosses the anterior part of the limbus, and, in *L. muralis*, medially touches the anterior part of the basilar membrane before terminating in the anterosuperior part of the periotic sac.

Small in both species, the intracapsular part of the periotic sac is in contact with the basilar membrane and posterior part of the limbus laterally, and extends freely downward through the periotic foramen. It is interesting to note that, in *L. muralis*, the intracapsular part of the sac is situated posterior to the level of the posterior margin of the footplate, while in *L. vivipara*, it lies directly opposite the footplate. Despite this difference, however, a line extended, in either species, from the center of the footplate through the center of the periotic foramen, passes through the central part of the basilar papilla.

Inferior to the periotic foramen, the extracapsular part of the periotic sac expands to occupy the recessus scalae tympani. Medially, it rests against the dura mater at the medial aperture of the recess, and, at the lateral aperture of the recess, it fuses with the mucosa of the tympanic cavity to form the secondary tympanic membrane. The latter is attached superiorly along, and for a short distance posterior to, the lateral margin of the periotic foramen, and, inferiorly, to the basis cranii. The membrane is larger than the footplate (considerably so in *L. vivipara*) and faces laterally into

the tympanic cavity. Its anterior limit lies inferior to the anterior margin of the footplate in *L. vivipara*, and inferior to the posterior margin of the same structure in *L. muralis*. In both species, the posterior limit of the membrane and extracapsular part of the periotic sac is reached at the level of the posterior extremity of the vestibular recess. The glossopharyngeal nerve traverses the posterior part of the medial aperture of the recessus scalae tympani and courses medial to the posterior part of the extracapsular extension of the periotic sac. No communication of periotic with cerebrospinal fluid cavities could be discerned.

Anguidae

(Figs. 32-34)

The saccule in *Ophisaurus* is markedly larger than the cochlear duct. Its anterior third extends rostral to the anterior limit of the lagena, and is housed, with the utricle, in the anterior part of the vestibular recess. This part of the saccule exaggerates the medial inclination of the superior margin shown by the remainder of organ, and is situated superolateral to the utricle. The entire superomedial saccular margin is attached to the vestibular roof by an extension of its membrana propria. The medial saccular wall, except in the region occupied by the macula, rests upon a layer of dense connective tissue resembling that of the limbus. Thickest toward the inferolateral saccular margin, the layer of connective tissue is attached anteriorly to the floor of the vestibular recess, and, posteriorly, blends with the superior margin of the posterior part of the limbus. As this union is approached, the posterior part of the saccule tapers slightly and, inferomedially, enters into the formation of a short laterally-compressed ductus reuniens; the latter appears to be a coalescence of the saccule and cochlear duct rather than a discrete structure. Associated with the medial wall of the ductus are the posterior extremities of the limbus and the saccular connective tissue layer noted above.

The cochlear duct extends anteroinferiorly from the ductus reuniens, its superior margin paralleling and immediately inferior to the inferolateral margin of the saccule; it occupies a relatively shallow cochlear recess. The lagena constitutes approximately the terminal half of the structure and is transversely expanded, relative to the posterior part. Both the basilar papilla and the heavy limbus are slightly elongated, and the latter shows a distinct ridge

on its lateral wall above the opening for the basilar membrane, in the position occupied by the limbic lip in gekkonoids.

The periotic cistern is large in *Ophisaurus*; it occupies the space in the vestibular and cochlear recesses lateral to, and along virtually the entire lengths of, the saccule and cochlear duct, including the lagena. The superior part contacts the thin superolateral wall of the saccule and extends medially at the anterior and posterior margins of that structure. Extending between these extremities, a channel passes longitudinally, medial to the saccule and in contact with its medial wall. Some diffuse periotic reticular tissue traverses the channel except at the base of the saccular macula; at that level it makes an additional communication with the major part of the cistern by way of the narrow opening between the adjacent walls of the saccule and cochlear duct. This series of channels resembles a scala sacculi, but it is here less clearly defined than in forms in which the term has been applied previously.

The inferior (cochlear) part of the periotic cistern is transversely narrowed; this is pronounced anteriorly and, just short of the anterior limit of the cochlear recess, a slight ridge of bone projecting medially from the superior lateral margin of the recess slightly constricts the saccular from the cochlear part of the cistern. The division is indistinct, however, and since no cisternal septum is present, no definitive scala vestibuli can be recognized. In the posterior extremity of the cochlear recess, opposite the ductus reuniens and posterior part of the cochlear duct, the periotic cistern is impinged upon by the elongate footplate of the columella auris.

The helicotrema originates directly from the periotic cistern in the rostral part of the cochlear recess. It arises immediately inferior to the ridge mentioned above and, grooving the anterior wall of the cochlear recess, curves medially, then posteriorly around the anterior extremity of the lagena. Projecting inferiorly from its lateral part is a small uncinata scala lagenae, which makes complete the contact of periotic fluid with the lateral surface of the lagena. Medially, the helicotrema is small and passes posteriorly, confined within a deep groove in the medial wall of the cochlear recess. It passes medial to the superior part of the lagena and lagenar ramuli of the posterior division of the auditory nerve. At the level of the anterior limit of the limbus, the helicotrema may be considered to terminate in the scala tympani, which expands laterally into a groove in the limbus. The scala itself is short and makes no

contact with the basilar membrane; it terminates in the antero-superior part of the periotic sac at the level of the anterior margin of the periotic foramen, opposite the anterior margin of the footplate of the columella auris.

The intracapsular part of the periotic sac is relatively small and constitutes a short vertically-expanded continuation of the scala tympani. Its posterior limit is opposite the posterior surface of the shaft of the columella auris. Superolaterally it is in contact with the basilar membrane and part of the limbus; inferomedially it abuts against the medial wall of the otic capsule. Extending posterolaterally and inferiorly through the periotic foramen, the intracapsular part of the sac continues into the expanded extracapsular part, the anterosuperior portion of which is housed in a furrow in the inferior surface of the posterior part of the otic capsule. Inferior and medial to the periotic foramen, and extending slightly caudal to its posterior limit, the extracapsular part of the periotic sac is related intimately to the meninges at the extremely large medial aperture of the recessus scalae tympani and, although possibly artefact, appears to bulge into the cranial cavity. Laterally, the extracapsular part of the sac fills the recessus scalae tympani and, at the lateral aperture of the recess, enters into the formation of the large secondary tympanic membrane, which forms part of the medial wall of the tympanic cavity. The membrane is situated inferior to the footplate and, tapering posteriorly, extends caudal to that structure to the level of the ampulla of the posterior semicircular canal. The membrane is crossed laterally by an artery, probably the internal carotid, and the posterior part of the periotic sac is related medially to the glossopharyngeal nerve.

Varanidae

(Figs. 35-37)

In approximately the posterior two-thirds of the otic capsule, the relationship of the vestibular to the cochlear recess is, in *Varanus*, much as it is in iguanid lizards; the two form a common chamber posteriorly, and are partially demarcated more anteriorly by a ridge of bone extending medially from the lateral superior margin of the cochlear recess. In the anterior third, however, the vestibular and cochlear recesses are separated by a horizontal plate of bone extending between them.

The saccule, roughly quadrangular when viewed from its superolateral aspect, extends rostrad into the anterior part of the vestibule.

lar recess for approximately one-fourth its own length. Here it is placed obliquely, its inferolateral margin attached to the floor of the recess and its superolateral margin attached to the roof. These attachments are made by the membrana propria, and are continued posteriorly, caudal to the dividing plate of bone, for approximately half the length of the saccule. The superior attachment continues along the medial part of the roof of the vestibular recess, and the inferior along the ridge of bone marking the lateral superior limit of the cochlear recess. Both the ridge and saccular attachment are absent caudal to the level of the posterior margin of the posterior acoustic foramen. Caudal to this level, the saccule becomes more nearly vertical, tapers posteriorly and, posteromedially, blends into a wide laterally-compressed ductus reuniens. The latter can only arbitrarily be designated, for in fact, it houses the posterior extremities of the saccular macula and basilar papilla, and is closely associated with the posterior part of the limbus.

The cochlear duct extends anteroinferiorly and slightly medially from its communication with the saccule. It is long and laterally compressed except at its laganar extremity, which is somewhat expanded medially. A heavy limbus is associated with the medial wall of the duct and blends into only slightly less dense periotic reticulum associated with the medial wall of the lagena. The basilar membrane and papilla are elongate, and superior to these structures, a low laterally-projecting ridge of limbic tissue supports a long tectorial membrane.

That part of the periotic cistern common to the saccule and cochlear duct extends rostrad from the posterior limit of the vestibular and cochlear recesses to the level of the posterior limit of the lateral attachment of the saccule. Medially it contacts the posterior parts of the saccule and cochlear duct, and the ductus reuniens. Laterally, the transversely-narrowed, inferior part of the cistern is impinged upon by the triangular footplate of the columella auris. The saccular part of the cistern extends anteriorly, superolateral to the saccule, past the anterior limit of that structure. The cochlear part of the cistern extends anteriorly, beyond the posterior limit of the lateral saccular attachment, as the scala vestibuli.

The exact limits of the scala vestibuli are difficult to determine in *Varanus*, and must be designated rather loosely. Laterally, the channel is clearly defined, posteriorly, by a short cisternal septum extending from the inferolateral margin of the saccule to the ridge

along the superior margin of the cochlear recess, and, more anteriorly, by direct contact of the saccule with that ridge. Because of the lateral extension of the saccule, however, its inferomedial wall forms part of the roof of the scala vestibuli as the latter extends superomedially in contact with the vestibular membrane. Furthermore, from the anterior part of the periotic cistern and the adjacent posterior part of the scala vestibuli, a periotic channel extends superomedially, past the superior margin of the cochlear duct, in contact with the remainder of the inferomedial wall of the saccule. This channel strongly resembles the scala sacculi noted in the gekkonoids, particularly that of *Aristelliger*, for here also, it extends anteriorly and communicates with the periotic cistern anterior to the saccule.

Anteriorly, just short of the bony division of the vestibular and cochlear recesses, the scala vestibuli terminates in the helicotrema. This channel is large and represents only a slight reduction in size from that of the scala vestibuli; it is housed in a wide shallow groove as it curves medially around the anterior margin of the cochlear duct, in contact with that structure. Laterally, the terminal part of the scala vestibuli and the helicotrema give off a scala lagenae, which extends inferiorly to contact the entire lateral wall of the lagena. Medially, the helicotrema follows a short course posterosuperiorly, passing between the medial wall of the cochlear recess and anterior parts of the cochlear duct and limbus. At the level of the caudal margin of the posterior acoustic foramen, inferior to the posterior part of the cochlear ganglion, it terminates in a short scala tympani. The latter enlarges abruptly by expanding laterally to occupy a channel in the limbus, and abuts against the anterior part of the basilar membrane. Upon reaching the anterior margin of the periotic foramen, the scala tympani may be considered to terminate in the periotic sac.

A constriction in the area where it traverses the periotic foramen rather clearly defines intra- and extracapsular parts of the periotic sac. The intracapsular part is an expanded prolongation of the scala tympani. It rests medially against the inferior part of the medial wall of the cochlear recess, and, laterally, is in contact with parts of the limbus and the basilar membrane. Posteriorly, the intracapsular part of the sac extends superiorly, following the steep ascent of the basilar membrane toward the ductus reuniens. Caudal to the posterior margin of the periotic foramen, a diverticulum of the sac continues in relationship to the basilar membrane. This

diverticulum is similar to the accessory scala tympani of gekkonoids, and I recognize it by the same name. As in the other group, it occupies a groove in the lateral surface of the limbus while, tapering, it abuts against the basilar membrane to the posterior limit of that structure.

Immediately inferior to its exit from the periotic foramen, the extracapsular part of the periotic sac is related medially to the small medial aperture of the recessus scalae tympani. In *Varanus* the latter contains a considerable amount of loose connective tissue and the periotic sac is, therefore, separated from the dura mater rather than in contact with it. The glossopharyngeal nerve exits from the cranial cavity through this opening and courses posteriorly, passing medial to the extracapsular part of the sac. The part of the sac related to the two foramina is small; from this region, it expands laterally and posteriorly within the recessus scalae tympani and extends to the medial wall of the tympanic cavity. Here it fuses with the mucous membrane to form a large triangular secondary tympanic membrane located immediately inferior to the footplate of the columella auris. The membrane is crossed diagonally by an ascending artery of medium size. This vessel is probably the internal carotid artery, but it cannot be traced far enough in my material to verify this identification.

Suborder OPHIDIA

Colubridae

(Figs. 38-41; 50)

Form and organization are rather constant in the otic labyrinths of the colubrids investigated, and are essentially similar to conditions described by Retzius (1884) in several other ophidians. The saccule, considerably larger than the cochlear duct, is oriented obliquely in the vestibular recess with its superior margin inclined distinctly toward the median plane. The inferolateral border of the saccule touches and attaches to the superior surface of the cochlear duct throughout most of the length of the latter, but does not significantly overhang the lateral surface of that structure. The membrana propria of the inferomedial saccular wall is thick, and a lamina of periotic connective tissue extends superomedially from it to attach to the roof of the vestibular recess. Anteriorly, the saccule extends rostral to the cochlear duct and is housed, with the utricle, in the anterior part of the vestibular recess; here, it is attached ventrolaterally, either by direct contact of the inferomedial

membrana propria with the vestibular floor, or by a periotic membrane extending between the two structures. Superior to the anterior part of the cochlear duct, a lateral saccular attachment is made by a cisternal septum, which extends from the membrana propria to attach along a slight longitudinal ridge on the internal surface of the elongated anterior part of the footplate of the columella auris. Posteriorly the saccule tapers, narrows and grades into the short elliptical ductus reuniens, which descends to merge with the posterior extremity of the cochlear duct.

Erect in the broad shallow cochlear recess, the cochlear duct extends anteriorly from the ductus reuniens and curves slightly medially toward its anterior extremity. The posterior part of the duct (*pars basilaris cochleae* of Retzius) has the form of an irregular cone, the base of which expands anteroinferiorly toward the lagena; the latter constitutes slightly more than the anterior half of the cochlear duct. The limbus is "C-shaped" and extends to associate itself with part of the lagena as well as with the basal part of the cochlear duct. The vestibular membrane extends between the lateral open arms of the structure, facing the inferior half of the footplate laterally, and the basilar membrane and lagenar macula medially.

The major cavity of the periotic cistern abuts against the lateral surfaces of the ductus reuniens and the posterior extremities of the saccule and cochlear duct. It is impinged upon posteriorly and inferolaterally by the posterior half, approximately, of the footplate of the columella auris, and extends anteriorly along the superolateral surface of the saccule. Excluded from the cochlear recess by the cisternal septum, the saccular extension of the cistern is in contact, inferolaterally, with the superior part of the anterior extremity of the footplate, and extends past the anterior margin of that structure into the anterior extremity of the vestibular recess.

The scala vestibuli arises from the anterior margin of the cochlear part of the periotic cistern opposite the anterior margin of the basilar membrane. This level marks the posterior limit of the cisternal septum, which forms the major part of the scalar roof and separates the scala from the overlying saccular part of the periotic cistern. Approximately triangular in cross section and tapering anteriorly, the scala vestibuli extends rostrad in contact with the thin superior part of the lateral wall of the lagena. It rests, laterally, against the inferior part of the anterior extremity of the footplate, and terminates in the helicotrema just rostral to the anterior margin

of the fenestra ovalis (vestibuli). Neither scala lagenae nor scala sacculi can be identified in any of the forms investigated.

Originating as a direct continuation of the scala vestibuli, the helicotrema is situated in a distinct groove in the lateral, anterior and medial walls of the rostral extremity of the cochlear recess. In this location it hooks medially around the anterior extremity of the lagena and comes to lie in the dense periotic tissue adjacent to the superomedial margin of that structure. The medial limb of the helicotrema extends caudally, directly opposite the scala vestibuli, for the full length of the lagena. In this part of its course it passes medial to lagenar ramuli of the posterior division of the auditory nerve, and inferior to the nerve itself. It terminates in the scala tympani at the level of the caudal margin of the posterior acoustic foramen.

Throughout its course in the cochlear recess, the scala tympani is housed in an enlarged extension of the groove accommodating the helicotrema. At its origin from the latter, the scala expands laterally into limbic tissue and touches the basilar membrane; variable vertical enlargement, corresponding to the vertical dimension of the basilar membrane, also occurs but is not great in any of the forms examined. In contact with the full length of the basilar membrane, the scala tympani passes medial to the basilar part of the cochlear duct, and courses beyond it to the inferomedial part of the posterior extremity of the cochlear recess. Here it exits from the otic capsule via the periotic foramen; actually forming a short canal in the forms investigated, the foramen opens caudally into the superior aspect of the recessus scalae tympani. Within the recess the scala tympani terminates in the periotic sac, which is entirely extracapsular.

Although the term "recessus scalae tympani" appears rather regularly in descriptions of the auditory region in ophidians, there appear to be divergences of opinion concerning the relationships, extent and limitations of the structure. For reasons of clarity, therefore, it seems desirable to define the manner in which it is used here, and to describe briefly its relationships to auditory structures in the forms examined. Medially, the posteroinferior relationships of the otic capsule do not differ radically from those in lizards. The periotic foramen, although placed more posteriorly than in most lizards, opens into a recess representing the anterior part of the metotic fissure; the recess communicates with the cranial cavity via an opening traversed by the glossopharyngeal nerve. These struc-

tures undoubtedly represent part of the recessus scalae tympani and its medial aperture.

The lateral aperture of the recess is considerably altered by modifications in the position and structure of the fenestra ovalis (vestibuli). Articulated in the fenestra, which is in the posterolateral aspect of the otic capsule, the external surface of the footplate faces inferolaterally, its inferior margin approaching the median plane of the cochlear recess. Encircling the footplate is a crest of bone (Fig. 38) elaborated by the prootic and opisthotic (fused with the exoccipital). The posteroinferior part of this *circumfenestral crest*, formed by the opisthotic, crosses the usual lateral aperture of the recessus scalae tympani and divides it into two openings. One looks posteriorly into the posterior part of the old metotic fissure; through this, the glossopharyngeal nerve exits from the recessus scalae tympani and joins the vagus nerve, with which it exits through the vagus foramen. The second opening faces anterosuperiorly and connects the recess with the fossa formed external to the footplate by the circumfenestral crest.

That part of the periotic sac occupying the recessus scalae tympani is small, since the restricted nature of the recess allows for expansion to a size only slightly greater than the diameter of the scala tympani. Medially, the sac is in contact with the dura mater at the medial aperture of the recess; the area of this contact is small in *Thamnophis*, *Diadophis* and *Lampropeltis*. In *Carphophis*, the area of contact and the medial aperture are, relatively, much larger, but neither in this genus, nor in the others, is any communication discernable between the periotic and cerebrospinal compartments.

At the lateral extremity of the recessus scalae tympani, the periotic sac turns anterosuperiorly and, traversing the second opening described above, enters the fossa situated lateral to the footplate and encircled by the circumfenestral crest. Here it expands, occupies the fossa fully, and lies against the external surface of the footplate. This terminal expanded part of the periotic sac has been described by de Burlet (1934) as the "pericapsular sinus." For reasons cited below, the term *juxtastapedial sinus* seems more appropriate, and the name *juxtastapedial fossa* might well be applied to the bony cavity it occupies.

Externally, at the mouth of the juxtastapedial fossa, the wall of the sinus is thickened by a fibrous layer and is attached to the circumfenestral crest. The membrane so formed is pigmented and

faces the internal surface of the mandibular musculature. In *Thamnophis*, *Diadophis* and *Lampropeltis* the membrane and the mouth of the juxtastapedial fossa are of approximately the same size as the footplate. In *Carphophis*, however, the size of the membrane and of the mouth of the fossa is reduced to approximately half the area of the footplate by accentuation of the inferior part of the circumfenestral crest; the long narrow membrane in this form faces only the superior half of the footplate.

Chelonia

(Figs. 42-45; 49)

Although two families were represented by the forms investigated, the differences shown in the internal ear do not seem to indicate their separate consideration here. All specimens showed the posterior placement of the cochlear duct, which has been noted repeatedly (Hasse, 1873; Retzius, 1884; de Burlet, 1934; and others), and which considerably affects the organization of the periotic channels.

Situated inferior to the utricle, the saccule lies adjacent to the medial wall of the vestibular recess and opposite the anterior two-thirds of the footplate of the columella auris. The lateral wall of the saccule touches the lateral vestibular wall anterosuperior to the footplate in *Chrysemys*; in *Pseudemys*, a space approximately equal to the width of the saccule intervenes between the two surfaces, and in *Chelydra* the saccule is confined to the medial third of the vestibular recess.

In all forms, the inferior margin of the saccule is attached to the floor of the vestibular recess and, more laterally, to the inferior part of the footplate by rather diffuse periotic reticulum. The attachment to the footplate is elaborated along the posterior margin of the saccule. Here, a lamina of denser reticular tissue extends laterally from the saccular membrana propria and the periotic reticulum between the saccule and cochlear duct; this lamina attaches to the vestibular floor immediately anterior to the bony cochlear recess, and continues laterally to make a narrow vertical attachment to the internal surface of the footplate at the junction of the posterior and central thirds of that structure. Taking the form of a cribrate septum, this laminar attachment essentially completes the separation of vestibular and cochlear recesses inferior to the ductus reuniens. Wever and Vernon (1956) mention attachments of the footplate to the saccule in turtles, and call them "stapedo-saccular strands." Although this term undoubtedly includes the

attachments described above, its authors apparently did not appreciate the definitive form shown by the periotic tissue with which they were dealing. The medial attachments of the cribrate lamina, and its relationships to the parts of the otic labyrinth and to the vestibular and cochlear recesses, are similar to those of the cisternal septum of most lizards; that term (cisternal septum) will, therefore, be used here.

Posteriorly the saccule communicates freely with the cochlear duct by way of a short elliptical ductus reuniens. The cochlear duct extends inferiorly, curving slightly medially toward its inferior extremity. The lagena constitutes approximately the inferior third of the structure and is expanded medially. A heavy limbus is associated with the entire medial wall of the cochlear duct; centrally, it accommodates the basilar membrane.

The large periotic cavity situated lateral to the saccule and cochlear duct is rather definitely limited above, and excluded from contact with parts of the superior division of the otic labyrinth, by a periotic membrane backed by the loosely organized periotic reticulum in which those parts are embedded. Although usually described as a single periotic chamber, the periotic (perilymphatic) cistern, the cavity is actually divided ventrally into two parts by the cisternal septum. This division creates relationships of periotic spaces to saccule and cochlear duct which are quite similar to those noted in most lizards. That part of the cavity anterior to the septum abuts against all (part in *Chrysemys*) of the thin lateral wall of the saccule, and extends posteriorly adjacent to the lateral wall of the ductus reuniens and superior part of the cochlear duct; these relationships make it seem appropriate to restrict the term periotic cistern to the anterior and superior parts of the cavity. That part situated posterior to the cisternal septum abuts against the lateral wall of the cochlear duct (vestibular membrane) and seems to merit the name scala vestibuli. Thus, the anterior two-thirds of the footplate abuts against the saccular part of the periotic cistern; the posterior third of the footplate impinges upon the scala vestibuli. A distinct channel extends ventrally from the scala vestibuli and hooks beneath the lagena in embryos of *Chrysemys*. This channel, which resembles a scala lagenae, is not present in any of the adult turtles examined.

The helicotrema arises from the inferomedial part of the scala vestibuli in the angle formed at the junction of the anterior margin of the lagena with the cisternal septum. It curves anteromedially,

traversing the periotic reticulum posteroinferior to the saccule, then, medial to the posterior part of the saccule, inclines antero-superiorly to a position inferior to the posterior acoustic foramen. Here it forms a genu by turning superiorly, then abruptly posteriorly beneath the cochlear ganglion and lateral to the inferior margin of the posterior acoustic foramen. It extends caudally, embedded in periotic reticulum adjacent to the medial wall of the otic capsule, and passes medial to posterior saccular, cochlear and lagenar ramuli of the posterior division of the auditory nerve. The helicotrema terminates by opening into the scala tympani at the anterior margin of the limbus, opposite the cisternal septum and posterior part of the footplate.

Immediately after its origin, the scala tympani expands laterally and superiorly into limbic tissue and lies against the vertically-oval basilar membrane in the central part of the cochlear duct. The scala narrows somewhat at the posterior limit of the membrane, then continues caudad, embedded in limbic tissue, medial to the posterior part of the cochlear duct. At the posterior limit of that structure, the scala tympani emerges from the limbus and enters the periotic reticular tissue occupying the posterior extremity of the cochlear recess. At this level, it lies immediately inferior to the internal glossopharyngeal foramen, and is crossed superiorly by the glossopharyngeal nerve. Immediately posterior to this, the scala tympani traverses the periotic foramen in the caudal wall of the cochlear recess and terminates in the periotic sac.

The periotic sac is situated in a space termed by Nick (1912) the "ductus hypoperilymphaticus"; the space is further considered by de Beer (1937) who follows Nick in terminology but suggests that, "The cavity of the ductus hypoperilymphaticus would then be merely an enclosed portion of the recessus scalae tympani." Except in that I am unable to find an opening of the space toward the cranial cavity "immediately in front of the jugular foramen" (de Beer, 1937:255), its relationships are as described by that author, and resemble those of the posterior part of the recessus scalae tympani in most other reptiles. It would seem logical, therefore, to apply the term recessus scalae tympani to this space in chelonians, realizing in so doing that it represents only part of the homologous structure in other reptiles.

Expanding within the recess, the periotic sac extends posteriorly to the level of the posterior margin of the vagus (jugular) foramen, where it ends blindly. Anteriorly, the medial wall of the periotic

sac is related to the medial bony wall of the recess; the posterior half, approximately, of the medial wall faces the cranial cavity at the vagus (jugular) foramen. Here the sac is crossed superiorly by a large vein and medially by the vagus nerve. Where it faces the foramen, the medial wall of the periotic sac is not well defined, but appears to be formed by a thin continuation of the lining of the remainder of the sac, backed by loosely organized tissue resembling periotic reticulum; the latter rests medially against a second thin membrane (dural?) which spans the vagus foramen at its internal margin. Although the appearance of this arrangement suggests that the periotic compartment may communicate with that of the cerebrospinal fluid, experimental replacement injections of Evans Blue dye in living anesthetized specimens of *Pseudemys* failed to pass either from the periotic sac into the cerebrospinal fluid, or from cerebrospinal fluid into the periotic spaces. Radiographic examinations of several specimens following perfusion with mercury (method of Young, 1952) further indicated that the periotic sac does not communicate with the cerebrospinal fluid compartment.

Laterally, within the recessus scalae tympani, the periotic sac abuts against the medial wall of the compartment termed by de Burlet (1934) the "pericapsular sinus"; I find this relationship clear in all specimens of the three genera examined. From its blind posterior extremity, which extends to the posterior extremity of the periotic sac, this sinus extends anteriorly to enter the recessus cavi tympani (Romer, 1956) lateral to the periotic foramen and diverges from the periotic sac. Within the recessus cavi tympani and forming its major content, the sinus extends anteriorly adjacent to the lateral wall of the otic capsule. Lateral to the footplate of the columella auris, the lateral surface of which it lies against, the sinus is traversed by the shaft of the columella. Anterior to this, at the level of the anterior margin of the fenestra ovalis (vestibuli), the sinus ends blindly.

In fresh material, this sinus is filled with a clear viscous fluid which is, subjectively, unlike either periotic or cerebrospinal fluid. In fixed and sectioned material, the contents of the sac shrink, fail to occupy the sinus completely and form a homogeneous translucent mass which stains blue with Mallory's technique, or pale green with the Patay-Masson method cited by Gray (1954). Replacement injections of Evans Blue dye made into this sinus fail to enter either the periotic or cerebrospinal fluid, and, conversely, dye in the cerebrospinal or periotic fluid does not color the fluid

of the sinus. It is, therefore, apparently a closed compartment and, in this respect, unlike the juxtastapedial sinus of colubrids. Further indication that this structure in turtles is not homologous to the ophidian sinus is found in embryos of *Chrysemys* in which the sinuses of the right and left sides communicate via a canal passing between the basisphenoid and parasphenoid primordia at the level of the external glossopharyngeal foramen. Therefore, believing this sinus to be no more than analogous to the juxtastapedial sinus of ophidians, and rejecting de Burlet's (1934) "pericapsular sinus" on the grounds that the term is misleading, I suggest that it be termed *paracapsular sinus*.

CROCODYLIA

Crocodylidae

(Figs. 46-47)

The general organization and histology of the internal ear in *Alligator* are covered in considerable detail by Retzius (1884), but his observations on the periotic channels, although accurate, are incomplete. The periotic system in *Crocodylus* receives special attention from de Burlet (1929, 1934), and his interpretation has been generally accepted as representative of the condition in the crocodylids. Although these authors, particularly the former, mention the relationships between the saccule, cochlear duct and otic capsule, these relationships profoundly influence the organization of periotic channels and differ sufficiently from those in other reptiles to merit brief consideration here.

In both *Alligator* and *Caiman* the saccule is of moderate size, slightly compressed transversely, and has the form of a rounded oval when viewed from its lateral aspect. Situated well medially in the vestibular recess, its thick medial wall is related to the capsular wall inferiorly and to the utricle superiorly; the lateral saccular wall is thin. Posteriorly, the saccule gives rise to a short elliptical ductus reuniens, which hooks inferolaterally to join the cochlear duct.

The latter is composed of two distinct limbs. From the junction with the ductus reuniens lateral to the posteroinferior part of the saccule, the proximal limb of the cochlear duct slopes anteroinferiorly through the vestibular recess to an area just lateral to the posterior acoustic foramen; here a genu is formed and from it the distal limb of the duct extends abruptly inferiorly into the deep, tubular, cochlear recess. The distal limb is slightly longer than the

proximal, and houses the lagenar macula in its terminal, slightly expanded, blind end. As pointed out by Retzius (1884), the vestibular membrane ("tegmentum vasculosum") and the limbus ("Knorpelrahmen der Pars Basilaris") spiral subtly and shift their relationships throughout the length of the cochlear duct. In general, however, the vestibular membrane may be said to form the superomedial wall of the proximal limb of the cochlear duct and the anterior wall of the distal limb; the limbus (and contained basilar membrane) form the inferolateral wall of the proximal limb, and the posterior wall of the distal limb.

Situated in the fenestra ovalis, superolateral to the cochlear duct, the footplate of the columella faces inferomedially toward that duct and the posteroinferior part of the sacculle. Immediately postero-inferior to the fenestra, the periotic foramen perforates the posterolateral wall of the otic capsule, lateral to the posterior part of the proximal limb of the cochlear duct. The superior margin of the periotic foramen, easily defined, is formed anteriorly by the narrow strut of bone which forms the inferior margin of the fenestra ovalis; the anterior and posterior margins are, likewise, readily identified. The inferior margin is, however, obscured by its intimate relationship to the base of the processus subcapsularis (of de Beer, 1937).

Internal to those openings, the limbus makes attachments which result in a longitudinal division of the vestibular recess and extend to subdivide the cochlear recess. The lateral margin of the limbus attaches to the internal surface of the strut of bone between the fenestra ovalis and periotic foramen; anterior to that strut, the lateral attachment is continued beneath the fenestra ovalis to the posterior margin of the cochlear recess, and, posteriorly, it continues superior to the periotic foramen. Posterior to that opening, the limbic attachment sweeps inferomedially across the posterior wall of the vestibular recess, then turns rostrally along a slight ridge which runs anteriorly to the medial margin of the mouth of the cochlear recess. Both medial and lateral attachments continue into the latter; here the medial attachment is the stronger, but both continue to a level just short of the superior limit of the lagena. Thus, these attachments define one space which lies superomedially in the vestibular recess and extends into the anterior part of the cochlear recess, and a second which reaches from the vicinity of the periotic foramen into the posterior part of the cochlear recess.

The periotic cistern lies in the superomedial of these two cavities. Irregularly triangular in transverse section, the cistern is in contact

with the lateral wall of the saccule, and inferolaterally rests against the vestibular membrane of the proximal limb of the cochlear duct. The third, superolateral, wall of the cistern abuts against the lateral wall of the vestibular recess, and, more inferiorly, against the footplate of the columella auris. The latter is so oriented that it faces directly toward the inferomedial part of the cistern. A short saccular part of the cistern extends rostrally into the anterior extremity of the vestibular recess, completing the cisternal contact with the lateral saccular wall. In my material, including late embryos and young specimens of *Alligator* and *Caiman*, I have been unable to find any periotic channel corresponding to the "ductus brevis" described by de Burlet (1929) in *Crocodylus*. Except in sections showing artefacts of fixation or sectioning, the periotic cistern appears to be without any direct communication with the periotic compartment corresponding to that author's "scala tympani."

The scala vestibuli arises from the anteroinferior extremity of the periotic cistern and extends ventrally into the cochlear recess. Situated anterolateral to the distal limb of the cochlear duct, the scala is irregularly crescentic in cross section, and lies in contact with the vestibular membrane and the lateral surface of the limbus of the distal limb. In the depths of the recess, an extension of the scala vestibuli expands anterolaterally into a small bony recess opposite the thin anterolateral wall of the lagena. This extension of the scala abuts against the lagena opposite the lagenar macula and probably corresponds to the scala lagenae of lacertilians.

The helicotrema arises from the scala vestibuli superior to the upper limit of the lagena. It extends medially from the posterolateral part of the scala and, grooving the lateral margin of the limbus, traverses the attachment of that structure to open, posterior to it, into the scala tympani.

At the level where it is entered by the helicotrema, the scala tympani is situated in the posterior cavity of the cochlear recess, bounded medially and laterally by the limbus and its attachments, and in contact with the basilar membrane anteriorly. Just inferior to this level, the medial and lateral parts of the limbus are united by a curved plate of limbic tissue, which is associated with the terminal part of the cochlear duct. An inferior extension of the scala tympani passes anterior to this plate and extends downward between it and the lower extremity of the basilar membrane; the extension terminates blindly at the level of the inferior limit of the basilar papilla. This scalar extension, which can be interpreted as an accessory scala tympani, is described and figured by Retzius (1884).

Attention should be called, however, to the fact that Retzius incorrectly believed a periotic space posterior to the limbic plate at this level to be the scala tympani; this is actually not the case, for my material shows conclusively that the area is closed from the tympanic scala by the firm attachment of the plate to the posterior wall of the cochlear recess immediately inferior to the helicotrema. The terminal part of the limbus and cochlear duct are but loosely attached to the posteromedial wall of the recess, and by some sparse periotic reticulum posteriorly; the space remaining is in lateral communication with the terminal part of the scala vestibuli.

The scala tympani extends superiorly in the cochlear recess, retaining the relationships noted at the level of the helicotrema. At the genu of the cochlear duct and limbus, the scala turns caudad and immediately terminates in the periotic sac. The intracapsular part of the sac is larger than the scala tympani and occupies the space inferolateral to the proximal limb of the cochlear duct. It is in contact with the basilar membrane superomedially. A narrow, short, blind extension of the sac invades the thick posterior part of the limbus to reach the posterior extremity of the basilar membrane. This blind extension, like the one at the distal extremity of the scala tympani, is described and figured by Retzius (1884), and can also be defined as an accessory scala tympani.

Laterally, the periotic sac traverses the periotic foramen and expands into the space delimited by the processus subcapsularis (of de Beer, 1937) and situated lateral to the posteroinferior part of the otic capsule. Anterosuperiorly, at the fenestra pseudorotunda (of de Beer), the extracapsular part of the sac touches and fuses with the mucosa of the tympanic cavity to form the large oval secondary tympanic membrane. Attached medially to the external surface of the strut of bone separating the fenestra ovalis from the periotic foramen, the membrane lies immediately posterolateral to the footplate of the columella auris and faces anterosuperiorly into the tympanic cavity. Posteroinferiorly, the sac bulges medially, enclosed between the processus subcapsularis and the posteroinferior wall of the otic capsule. Extending toward the cranial cavity, this part of the periotic sac lies anterior to the ganglion of the vagus nerve and is in intimate medial association with the glossopharyngeal nerve. The sac itself does not reach the dura mater, but a strand of loose connective tissue resembling periotic reticulum does extend from its medial wall to attach to the dura immediately adjacent to the point of exit of the glossopharyngeal nerve.

DISCUSSION

As represented by the forms included in this investigation, the sacculo-cochlear (inferior) division of the reptilian periotic labyrinth consists of: (1) a variably-divided intracapsular body of periotic fluid interposed between the footplate of the columella auris and the vestibular membrane of the cochlear duct; (2) a narrow curved channel, here termed the helicotrema, which connects the above with (3) a broad channel and/or sac associated with the basilar membrane, the periotic foramen, the glossopharyngeal nerve and remnants of the embryonic metotic fissure; and (4) specialized periotic diverticula associated with the receptor areas of the saccule and cochlear duct. The fluid contained within these channels and compartments extends to fill spaces in the periotic reticulum of the superior division of the otic labyrinth, but does not communicate (unless by way of selectively permeable membranes) with either otic or cerebrospinal fluid compartments.

This general organization of parts of the periotic labyrinth seems entirely compatible with that which might be expected of an ancestral stock derived from an amphibian line and leading eventually to mammals. Accounts by Retzius (1881), Harrison (1902) and de Burlet (1929, 1934) indicate that comparable parts and organization are present in the ear of recent amphibians. A periotic (perilymphatic) cistern is situated between the equivalent of the footplate and the lateral wall of the saccule, and is connected with a medially-placed periotic (perilymphatic) sac by a long narrow helicotrema (perilymphatic duct) which passes in intimate relationship to the lagena. The periotic sac, although specialized in its mode of relationship to the receptor areas, is closed, and lies in an intracapsular and intracranial position immediately anterior to the vagus (jugular) foramen; in *Bombinator* and *Rana* a part of the sac extends externally through the vagus foramen (de Burlet, *ibid.*). Although the periotic systems of these animals show considerable specialization in detail, they could easily be derived from a system similar to that in *Sphenodon*. Romer (1956) postulates an organization of foramina in the medial wall of the otic capsule in primitive amphibians and reptiles (anthracosaurs, *Seymouria* and *Kotlassia*) virtually identical to the arrangement of similar openings in the otic capsule of *Sphenodon*. Extrapolating from these data, it seems reasonable to assume that the basic organization of the periotic labyrinth was established early in amphibian stock, and has remained relatively unchanged, despite the change in vibratory

receptors which are believed to have taken place during the evolution of the amphibians.

Aside from questions concerning the homology of the mammalian fenestra rotunda (cochleae), which appear to have been satisfactorily answered by de Beer (1929, 1937), the part to part relationship of the reptilian periotic labyrinth to that of mammals seems to have gone unquestioned in the literature. Referring to the morphology of the ear in crocodylids and birds, de Burlet (1934), Gray (1955) and others point out the simplicity of the cochlear channels in *Echidna* and compare them directly to those of (presumably) a reptilian ancestor. Under the generally-accepted conditions of communication of the periotic system with subarachnoid spaces in mammals (Bast and Anson, 1949; Wolff, Bellucci and Eggston, 1957; standard works on gross human anatomy and the mammalian ear) such a direct transition seems extremely unlikely, if not impossible. As noted above, the periotic sac in amphibians is described as a closed compartment, and the observations of this investigation have consistently indicated that there is no communication between the two compartments in any of the modern reptiles investigated. These observations find support (primarily in figures) in de Burlet's (1929, 1934) treatment of reptiles other than ophidians, and in the work of Shute and Bellairs (1953). It seems improbable that a system isolated from fluid interchange throughout a great part of its prior evolution would suddenly achieve such contact in mammals.

Suggestions that periotic and cerebrospinal fluids are not in communication in mammals do appear in the literature. Streeter's (1918) study of the development of the periotic spaces fails to show their communication with subarachnoid spaces, and the work of Waltner (1948) casts further doubt concerning the existence of such a communication. Young (1952 and personal communication) presents convincing evidence that the periotic (perilymphatic) duct in some mammals terminates in a small blind sac situated adjacent to the meninges in the jugular fossa. Using Young's procedure, I have been able to duplicate his results in human temporal bones, and in cats, dogs and rabbits. Experimental replacement injections of Evans Blue dye into the cysterna magna and vestibule in rabbits further indicate that the periotic system is not in free communication with the cerebrospinal fluid. This situation is that which might logically be expected if one assumes direct homology of the mammalian system with that of reptiles.

As suggested above, the periotic labyrinth of *Sphenodon* is considered to be the most primitive of those treated in this investigation, and might well be similar to that of some of the earliest known reptiles. Price (1935) and Romer (1956) point out the unossified condition of a part of the medial wall of the otic capsule in *Captorhinus*, an area similar to one in seymouriamorphs in which the latter author postulates a periotic foramen. Such placement, similar to that in *Sphenodon*, would allow for either an intracranial periotic sac such as is found in some amphibians, or for extension of such a sac through the adjacent large vagus foramen. Romer, in fact, states that such an extension may have accompanied the glossopharyngeal and vagus nerves in *Captorhinus*. Assuming this condition to have existed, the extension of the periotic sac almost certainly ended blindly in the suprpharyngeal region, since the external orifice of the vagus foramen in this and other primitive reptiles is placed in a position incompatible with the formation of a secondary tympanic membrane.

Some additional support may be inferred from the contents of the otic capsule. The periotic labyrinth of *Sphenodon* shows little specialization, bears a reasonable resemblance to that of modern amphibians, and would require the postulation of only a few changes for the derivation of the systems noted in the other reptiles investigated. The medial origin of the ductus reuniens from the sacculus is more reminiscent of the conditions described in amphibians than it is of the posterior or posteromedial placement found in other reptiles. Furthermore, the size of the basilar papilla in relation to the size of the lagenar and saccular maculae is less in *Sphenodon* than in other reptiles included in this study or recorded in the figures of Retzius (1884). Weston (1939) infers that this fact is indicative of the primitive nature of the auditory apparatus of *Sphenodon*.

Changes in the periotic labyrinth from the presumed primitive organization appear to be associated with alterations in the otic capsule and adjacent parts of the skull, modifications in size, position and attachments of the parts of the inferior division of the otic labyrinth, and changes in the size of the basilar papilla and lagenar and saccular maculae. Three major lines of evolution seem to be represented by forms considered in this investigation and correspond to the usual taxonomic grouping of the Squamata, Chelonia and Crocodylia. As noted below, the ophidians might be considered as forming a fourth line, as is implied by de Burlet (1934), but probably may be more properly considered as showing no more than a strong modification of the lacertilian pattern.

The most obvious "advance" shown by lacertilians is the formation of a secondary tympanic membrane. This is associated with a slightly more caudal placement of the periotic foramen than that shown by *Sphenodon*, and varying degrees of division of the metotic fissure into the definitive recessus scalae tympani and vagus foramen of the adult. In all lacertilians examined the periotic sac traverses the periotic foramen to enter the recess and form the secondary tympanic membrane within its confines. In most of the forms examined, the membrane is attached near the margins of the recess and faces directly into the tympanic cavity forming part of its medial wall. In the representatives of gekkonoid families and in *Cnemidophorus* (Teiidae), however, the periotic sac occupies only the superomedial part of the recess, and the secondary tympanic membrane faces inferiorly or inferolaterally into a deep pit in the medial tympanic wall formed by the unoccupied part of the recess. A similar situation is reported in *Ctenosaura* (Oelrich, 1956), and the condition in *Anolis* approaches this, but it was not found to be pronounced in any other iguanids considered here.

This variable location of the secondary tympanic membrane leads to an unfortunate confusion in the meaning of the term "recessus scalae tympani" when it is applied in lacertilians. In his definition of the space, de Beer (1937:431) states:

"In all Tetrapod vertebrates a diverticulum of the perilymphatic spaces of the ear emerges through the foramen perilymphaticum in the wall of the auditory capsule, and finds itself in an extracranial and extracapsular space, the recessus scalae tympani, situated in the anterior region of the fissura metotica. The recessus scalae tympani communicates with the cranial cavity through its apertura medialis which coincides with the anterior portion of the fissura metotica, and over its apertura lateralis is stretched the secondary tympanic membrane, which separates the recessus scalae tympani from the tympanic cavity."

Not only does this definition present problems (noted below) when applied in lacertilians in which the secondary tympanic membrane is deeply placed, but it also seems inapplicable either in forms lacking a true secondary tympanic membrane or in those in which the periotic sac terminates in, or traverses, the cranial cavity (amphibians; *Sphenodon*). Employing a more common, less restrictive interpretation, Romer (1956:118) says of the area in lizards, the only group in which he applies the term regularly:

"Anteroventral to the vagus foramen is the recessus scalae tympani, formed from the lower part of the embryological metotic fissure. The perilymphatic duct enters this recess from the ear capsule, sends one branch inward to the brain cavity and a second outward to a membrane facing the middle-ear cavity;

the structure is thus comparable to (but not strictly homologous with) the mammalian fenestra rotunda.”

These two definitions, the former based upon the position of the secondary tympanic membrane and the latter applied to a bony cavity, are compatible only when the periotic sac completely fills the cavity.

In his description of *Ctenosaura*, Oelrich (1956:17) solves the problem of the deeply-placed membrane as follows:

“Medial to the crista interfenestralis is a deep occipital recess, bounded posteriorly by the crista tuberalis (Säve-Söderbaugh, 1945, 1947) and ventrally by a similar recess in the basioccipital. In the occipital recess, near its apex, lies the foramen rotundum, marked by a small crest and covered by the membrana tympani secunda. Beyond this foramen in the cavity of the exoccipital is the small triangular recessus scala tympani, whose medial wall is the foramen perilymphaticus (Fig. 9), which opens into the cranial cavity, and on whose superior wall is the fenestra cochlea (Fig. 12), which opens into the medial surface of the lagenar recess. The recessus houses the terminal end of the saccus perilymphaticus and transmits the glossopharyngeal nerve.”

Disregarding divergences in the application of some terms, this approach conforms to de Beer's (1937) definition, but necessitates the introduction of the term “occipital recess” for the designation of the part of the fossa external to the secondary tympanic membrane. This does not seem desirable, since in this system the terms “occipital recess” and “recessus scalae tympani” designate different regions of a fossa which has commonly been recognized by the one (latter) name.

It seems that a satisfactory solution might be found for all forms in which a recessus scalae tympani exists by defining the space as— an extracranial and extracapsular fossa, derived from the anteroventral part of the metotic fissure, which communicates with the cranial cavity by way of a medial aperture and with the otic capsule by way of the periotic foramen, and which contains part or all of the periotic sac. Deliberately general, such a definition does not seem to conflict with the usage of the term in osteological literature, and allows sufficient flexibility for its application in forms in which the space is enclosed or unrelated to a true secondary tympanic membrane.

The relatively limited sampling precludes firm evaluation of the significance of deep placement of the secondary tympanic membrane within the recessus scalae tympani, but several items seem worthy of note. The geckos, in which the feature seems to be consistent, are commonly considered to be members of an archaic group (Shute and Bellairs, 1953; Romer, 1956), and Smith (1946) con-

siders *Ctenosaura*, in which Oelrich (1956) reports a deeply placed membrane, to be a primitive iguanid. According to Romer (*ibid.*) the teiids are a "relatively primitive family" of leptoglossans, a group which he regards as being "a 'higher' lizard assemblage." Shute and Bellairs (*ibid.*), however, point out similarities in the structure of the internal ear in *Tubinambis* to that in geckos; their observations find support, although less striking than that which they indicate, in a comparison of the teiid *Cnemidophorus* with the geckos considered here. Taken together, these things suggest that deep placement of the secondary tympanic membrane may be a relatively primitive lacertilian feature. Subjectively this is borne out, since deep placement of the membrane is associated with a medial or posteromedial placement of the periotic foramen, one which is more like that in *Sphenodon* than like the posteroventral or posterolateral placement noted in forms in which the secondary tympanic membrane is situated in the plane of the medial wall of the tympanic cavity. Furthermore, the association of the periotic sac with the dura mater tends to be intimate in forms with the membrane deep in the recessus scalae tympani; as noted above, the sac actually bulges into the cranial cavity in *Cnemidophorus*. These features could be interpreted as representing an intermediate stage between the presumed primitive, sphenodontid, condition and the relationships common in those forms in which the periotic sac fully occupies the recessus scalae tympani.

A second line of specialization in the lacertilian periotic labyrinth is indicated in the variable division of the periotic cistern which results in the formation of a scala vestibuli; this is usually accomplished by a cisternal septum and/or bony ridge marking the superior lateral margin of the cochlear recess. Some indication of development of these structures, with the resultant definition of a scala vestibuli, is found in all families of lizards investigated. Least marked in *Cnemidophorus* and *Ophisaurus*, in which only a short indistinct ridge is present, the separation shows varying degrees of completeness culminating in the situation noted in *Aristelliger*, in which the separation of the scala vestibuli from the saccular part of the periotic cistern is complete except for a narrow communication between the two in the posterior extremity of the otic capsule. Like the deeply-placed secondary tympanic membrane, the cisternal septum does not appear to be a feature which shows any continuous graded development throughout the lizards as a whole, but rather appears to have been developed progressively, and in a parallel fashion, in different groups. For example, the

iguanids *Crotaphytus*, *Sceloporus* and *Uta* show absence or weak development of the septum, while in *Phrynosoma* and *Anolis* the structure is marked, but shows differences in its degree of development and relationship to the fenestra ovalis. In gekkonoids examined the septum and ridge are consistently present but show variable degrees of development. In *Coleonyx*, the arrangement is similar to that in *Anolis* in that the division is anterior to the fenestra ovalis, but the ridge to which the septum attaches is more strongly developed than in iguanids. *Sphaerodactylus* has both septum and ridge anterior to the fenestra, but continues the ridge posteriorly for the full length of the cochlear recess. *Hemidactylus* and *Aristelliger* both have a complete ridge; in the former a cisternal septum is present and extends above the fenestra ovalis to a level caudal to the midpoint of that opening, while in the latter, direct attachment of saccular periotic tissue accomplishes the division of the periotic cistern to a level caudal to the fenestra ovalis. It should be pointed out that, although the position of the septum and ridge in gekkonoids is similar to that in other lizards, the contribution of bone to the division is greater than in other forms. Poorly marked division of the periotic cistern in *Cnemidophorus* and *Ophisaurus* coupled with the presence of a scala vestibuli in scincids, lacertids and varanids suggests that a progressive separation of the scala vestibuli from the periotic cistern may also have occurred in leptoglossans and diploglossans, but the material available does not warrant a positive statement on this point.

Generally speaking, the extent of development of the cisternal septum, or direct attachment of the saccule to the wall of the otic capsule, can be more directly correlated with the size and position of the cochlear receptors than it can with the function of fixation of the saccule and cochlear duct. Although the latter function is undoubtedly present, it appears to be secondary to that of delimitation of a scala vestibuli. Iguanids suggest this, for the basilar papilla is more strongly developed in *Anolis* and *Phrynosoma* than in other forms, and in these the cisternal septum is well developed. More convincing is the organization in the gekkonoids; in *Coleonyx* and *Sphaerodactylus*, in which the degree of development of the basilar papilla is less than that in the gekkonoids, the septum is present only anterior to the fenestra ovalis. On the other hand, in *Aristelliger* and *Hemidactylus* in which the basilar papilla is enlarged by extending posteriorly, the scala vestibuli can be defined in relationship to the entire lateral wall of the cochlear duct. In

scincids, elongation of the basilar papilla approaches that noted in geckos, but the receptor develops anteriorly rather than posteriorly. The scala vestibuli is present only anterior to the fenestra ovalis in the forms examined, but this position places it opposite the anterior part of the receptor. Thus, position of the receptor seems to be an important correlate to the degree of scalar development. It seems, therefore, that the differentiation of a scala vestibuli, either by a cisternal septum or by direct attachment of the saccule to the lateral wall of the vestibular recess, is associated with restriction or "channeling" of vibrations introduced by the footplate to the lateral wall of the cochlear duct opposite the basilar papilla and lagenar macula. Its structure and position in lizards seem entirely compatible with such a function.

The scala lagenae, prominent in *Sphenodon*, is reduced in all lacertilians examined. In iguanids, as noted earlier, the development of the channel correlates well with the size of the lagenar macula; this holds true, because in the specimens examined the scala lagenae constitutes the major periotic association of the lagenar macula. This association does not appear to be consistent through all groups of lizards; in the gekkonoids, for example, the lagenar macula lies opposite a scala lagenae, but is also associated with the scala vestibuli and the helicotrema. Generally speaking, the scala lagenae appears to be relatively consistent within families of lizards; in higher taxonomic assemblages, its development varies with the position of the lagenar macula in relation to the scala vestibuli or periotic cistern, as well as with the size of the receptor. Seemingly, the only generalization possible, concerning the structure in lacertilians as a whole, is that it is well developed in those forms in which the lagenar macula is large and distinctly ventral to the plane of the basilar papilla, and reduced in those forms in which the receptor is higher or smaller. Its sole function appears to be to extend the periotic cistern or scala vestibuli sufficiently to bring lateral periotic fluid channels into relationship with that part of the cochlear duct housing the macula lagenae. This is in itself interesting, however, for de Burlet (1929, 1934) states rather strongly that periotic channels are not related to the lagena, but are blocked from such association by periotic reticulum (his "Bindegewebsbalken").

The periotic channel here termed the scala sacculi was noted in eublepharids, gekkonids, lacertids, anguids and varanids. Although variable in its anterior and posterior communications, the channel is consistently related to the inferior part of the medial wall of the

sacculi and in communication inferolaterally with the scala vestibuli or corresponding part of the periotic cistern. These relationships are extremely similar to those of the inferomedial part of the periotic cistern (that part situated between the medial wall of the sacculi and opposing lateral wall of the cochlear duct) of *Sphendon*. A marked resemblance of the scala to the sphenodontid structure is present in *Varanus*, in which the ductus reuniens originates from the inferomedial wall of the sacculi and continues into a cochlear duct extending significantly more ventrally than anteriorly. Other forms show varying decreases in the freedom with which the channel communicates with the periotic cistern anterior and posterior to the sacculi, and reduction in the size of the lateral communication with the scala vestibuli or periotic cistern. The degree of isolation shown by the saccular scala correlates well with the relationship between the sacculi and cochlear duct; those forms in which the ductus reuniens originates more medially from the sacculi and extends into a ventrally-directed cochlear duct show freer communications than those forms in which the ductus reuniens originates posteriorly from the sacculi and the cochlear duct extends anteriorly beneath it. These things seem to indicate that the scala sacculi may well be derived from the inferomedial part of a primitive periotic cistern similar to that in *Sphendon*. Its formation has probably been associated with the shifting of the origin of the ductus reuniens from the medial to the posterior surface of the sacculi, and assumption by the cochlear duct of a position adjacent to the inferior margin of the sacculi.

It is noteworthy that the scala sacculi is most clearly defined and isolated from communication with the superior part of the periotic cistern in *Hemidactylus*, *Coleonyx* and *Lacerta*; in these forms, the scala extends as a clear channel only from the scala vestibuli to the base of the saccular macula. In *Coleonyx*, the central part of the lateral wall of the sacculi is thick, and in *Hemidactylus*, the entire lateral wall is thickened and attached to the wall of the vestibular recess. In *Lacerta*, the lateral wall of the sacculi is not structurally modified but does contact the lateral vestibular wall, excluding the periotic cistern from its typical contact with that part. These modifications, all resulting in alteration of the usual relationship of the periotic cistern, coupled with the intimate association of the saccular scala with the base of the macula sacculi, suggest that the scala may, in these forms at least, serve as a conducting channel for vibratory stimuli. Such a conclusion seems quite reasonable since the

works of von Frisch (1938) and Weston (1939) support interpretation of the saccular macula as a vibratory receptor (in part) in lower vertebrates. In his consideration of the structure, de Burlet (1929, 1934) questions its function and tentatively assigns it to both the equilibratory and auditory systems, largely on the grounds of the consistent association of the periotic cistern with the lateral wall of the saccule. Thus, although it is probably derived from a primitive periotic space and may, in some forms, be indicative of a primitive organization in the ear, the scala sacculi appears to form a highly specialized vibratory conducting channel in some lizards.

It is quite apparent that the periotic cistern and its derivatives are intimately linked ontogenetically (and probably phylogenetically) with the morphology of the saccule and cochlear duct, and with the size, shape and location of the three receptors they contain. Subjective observations made in connection with this study indicate that investigation of the general morphology of these structures, coupled with a detailed analysis of their receptors might yield valuable otological and taxonomic information.

The helicotrema in lacertilians is extremely consistent in its form and relationships; particularly stable are its relationships to the anterior extremity of the cochlear duct and to the posterior acoustic foramen. The degree to which it grooves the wall of the cochlear recess is variable and ranges from slight grooving of the anterior wall to the formation of a bony canal in the anterior wall of the cochlear recess. The latter condition was noted only in *Coleonyx* and *Sphaerodactylus*; the gekkonids examined showed only grooving comparable to that found in most other lizards.

The recognition of both a scala tympani and periotic sac may be questioned, since not only do the scala and intracapsular part of the sac form a morphological and functional continuum, but the works of de Beer (1929, 1937) rather clearly indicate that at least the intracapsular part of the sac is represented by part of the scala tympani in mammals. On the other hand, that part termed scala tympani is clearly differentiated from the intracapsular part of the periotic sac in lacertilians, and the latter can be only arbitrarily separated from the extracapsular part of the periotic sac; therefore, the recognition of both scala tympani and periotic sac in lacertilians seems justified on morphologic grounds.

The scala tympani and intracapsular part of the periotic sac show considerable uniformity in their relationships throughout the lacertilians examined. Occupying the space between the limbus and

basilar membrane laterally, and the wall of the cochlear recess and its periotic foramen, the channels do vary in size and shape in different forms. Differences noted seem to depend not only upon the attachments of the limbus and its relationship to the periotic foramen, but, particularly, upon the shape and degree of development of the basilar papilla and membrane. In most forms, variations in the form and relationships of cochlear structures may be considered minor, and are accompanied by minor changes in the form and size of the periotic sac. In eublepharids, gekkonids, varanids and scincids, however, the basilar papilla and membrane are elongate and are related to a special diverticulum of the periotic sac, here termed the accessory scala tympani. Shute and Bellairs (1953) report the presence of such diverticula in geckos, and Retzius (1884) records them in several skinks; the diverticulum has not been previously reported in varanids. Obviously a specialization to allow intimate relation of periotic fluid to the elongated basilar papilla and membrane of these forms, the accessory scala tympani extends from the intracapsular part of the periotic sac, traverse a groove in the lateral surface of the limbus and ends blindly at the limit of the basilar membrane. In scincids, the accessory scala extends rostrally from the anterior surface of the periotic sac and is situated ventral to the scala tympani and medial limb of the helicotrema; in the other families in which it is present, the accessory scala reaches postero-superiorly, and is undoubtedly analogous to the scincid channel. In *Varanus*, the accessory scala is aligned with the scala tympani and arises from the small intracapsular part of the periotic sac, while in representatives of the two gekkonoid families in which it was observed, the accessory scala arises from a large periotic compartment and forms a distinct angle with the scala tympani and medial limb of the helicotrema; aside from these differences, the structures are quite similar. Lacking information on the development of the accessory scala tympani in these families, one may conservatively assume that the varanid channel represents a modification of the periotic sac paralleling that in the two gekkonoid families.

Ophidians show relatively little modification of the intracapsular part of the periotic labyrinth. The periotic cistern, scala vestibuli and cisternal septum have relationships to the saccule and cochlear duct essentially like those in lacertilians in which the cochlear duct parallels the inferior margin of the saccule. The lateral relationships of these structures are, however, considerably altered by the relatively great size of the footplate of the columella auris. Con-

stituting a major part of the inferolateral wall of the otic capsule, the superior half of the elongated footplate faces into the vestibular recess, and the inferior half looks into the cochlear recess; the longitudinal midline of the footplate thus occupies a position equivalent to the position of the ridge marking the superior lateral margin of the cochlear recess in lacertilians. Extending laterally, the cisternal septum attaches to the internal periosteum of the footplate. The size of the footplate, coupled with its relationships to the cisternal septum and structures of the otic labyrinth lend attraction to ideas of capsular origin of the columella auris such as Möller's (1905), but evidence presented by de Beer (1937) against such an interpretation makes it seem more reasonable to assume that the relationship of the septum to the footplate has been otherwise acquired. The limited sampling of ophidians suggests that a cisternal septum may have been present in their ancestral stock, but the progressive development of the septum in different groups of lacertilians makes equally possible the assumption that snakes have developed the septum independently and that it has extended its attachment posteriorly onto the footplate.

The helicotrema and medial periotic channels show relationships identical to those in lacertilians, but the periotic sac is considerably reduced in size and appears attenuated as a result of the posterior placement of the periotic foramen. The slight enlargement of the scala tympani adjacent to the basilar membrane doubtless represents the intracapsular part of the sac, and communicates directly with the sacciform enlargement occupying the recessus scalae tympani; recognition of the homology by direct application of the terms used in lacertilians does not, however, seem desirable.

As recorded by de Burlet (1934), it is in the extracapsular part of the periotic system that ophidians diverge markedly from lacertilians. That author terms the entire extracapsular compartment the "pericapsular sinus" and reports a direct communication of this compartment with cerebrospinal fluid spaces (submeningealen Raum); although he is not explicit concerning the location of this communication, his figures indicate that it must occur through the opening recognized above as the medial aperture of the recessus scalae tympani. Apparently the fragile membranes covering the medial aperture of the recess in his material were destroyed in preparation, as frequently happens; lacking this, identification of the periotic sac within the recess is difficult, and one might logically reach conclusions such as de Burlet's. Actually, the relationships of the periotic sac at the medial aperture of the recess are identical

to those found in most lacertilians; de Beer (1937) reports similar findings, but notes minor variations in the relationship of the glossopharyngeal nerve to the sac and medial aperture of the recess. Such consistency in these relationships suggests that ancestral ophidians must have been derived from a stock in which the periotic sac occupied part of a definitive recessus scalae tympani, rather than from a more primitive one in which the periotic sac presumably traversed the cranial cavity and vagus foramen; only lacertilians show a directly comparable series of relationships.

The radical alteration of the lateral relationships of the periotic sac seems to be, in large part, attributable to the encroachment of the opisthotic upon the area of the lateral aperture of the recessus scalae tympani in the formation of the posterior part of the circumfenestral crest. Extending anteroventrally, the process crosses the usual lateral aperture and leaves two foramina. One of these looks posteriorly into the vagus foramen, is traversed by the glossopharyngeal nerve and can only be interpreted as representing the posterior part of the lacertilian lateral aperture. The anterior part of the lateral aperture is thus represented by the foramen situated posteroventral to the footplate of the columella auris and forms the communication between the recessus scalae tympani and the juxtastapedial fossa. Thus, the juxtastapedial sinus is actually an extension of the periotic sac outside the confines of the recessus scalae tympani, and occurs only in ophidians. The membrane formed at the mouth of the juxtastapedial fossa must, therefore, be analogous to the secondary tympanic membrane of lizards rather than homologous, as is suggested by de Beer (1937).

The suggestion is advanced by de Burlet (1934) that this arrangement probably constitutes a dampening mechanism, but he does not speculate concerning its mode of action. It is possible that the membrane may allow some dampening of vibrations in the periotic fluid against the mandibular musculature (and this concept finds indirect support in *Carphophis* in which the size of the membrane is reduced and the area of contact of the periotic sac with the dura at the medial aperture of the recessus scalae tympani is correspondingly enlarged), but it seems that the primary significance of this arrangement is that it allows a reciprocating movement of the columella auris and periotic fluid. Thus, inward movement of the footplate displaces periotic fluid, but at the same time provides for accommodation of displaced fluid by increasing the depth of the juxtastapedial fossa and sinus.

There is some evidence suggesting that the juxtastapedial sinus and fossa may undergo specialization in forms adapted to burrowing. Of the colubrids examined, *Carphophis* shows external characteristics more like those of true burrowing snakes than do the other forms, and I have observed some burrowing behavior in *Carphophis* in the field; the latter is not true of the other colubrids utilized in this investigation. The reduced size of the mouth of the juxtastapedial fossa in relation to the size of the footplate in a form showing these characteristics led to an attempt to ascertain the relationships in true burrowers. Examination of a skull of *Leptotyphlops* showed certain external similarities of the otic region in this form to that of *Typhlops*, as described by Haas (1930). Dissection of the area revealed that the shaft of the columella auris traverses a small opening similar to that designated as the fenestra ovalis in *Typhlops*, and extends internally across a small space before terminating in a distinctly enlarged footplate. A small foramen posteroinferior to the footplate was found to communicate with the cranial cavity. These relationships suggest that the circumfenestral crest has been elaborated in this form and has completely enclosed the juxtastapedial fossa and sinus, except for the small opening traversed by the shaft of the columella. The fossa and sinus would then be intracapsular in the sense that they are completely surrounded by laminae of the prootic and opisthotic, but would retain the same relationships to the footplate as those noted in colubrids. The external opening in the otic capsule of *Leptotyphlops* would, therefore, not be the fenestra ovalis, but the constricted mouth of the juxtastapedial fossa; Haas' (1930) description of *Typhlops* allows speculation that the same relationships may exist in that form. The functional implications of this situation are interesting since closure of the juxtastapedial fossa would result in total dependence upon the reciprocal type of fluid movement suggested above, plus the possibility of some dampening at the medial aperture of the recessus scalae tympani. Sections of complete heads of *Typhlops* and *Leptotyphlops* are now being prepared for study of the precise relationships of the fluid labyrinths.

Chelonians show major divergences in the organization of both the intracapsular and extracapsular parts of the periotic labyrinth. Primarily associated with the accentuated ventromedial direction of the cochlear duct, the periotic cistern, cisternal septum and scala vestibuli have almost vertical rather than horizontal relationships to the footplate of the columella auris. Thus, the periotic cistern is

impinged upon by the anterior and superior parts of the footplate, while the scala vestibuli rests against the posterior part of the same structure.

The cribrate lamina designated cisternal septum shows obvious differences in structure from the condensed lamina given the same name in lizards and snakes. Although it finds its medial attachment in the periotic reticulum between the saccule and cochlear duct and extends laterally to separate the cochlear from the vestibular recess, the septum is composed of rather loosely organized tissue bearing little resemblance to that noted in other forms. Furthermore, its continuity anteriorly with ventral saccular attachments finds no direct comparison in the Squamata. Its structure would allow the septum to function in the capacity of disrupting patterns of movement in the periotic fluid, but its relationship to the footplate of the columella auris is hardly compatible with such a function, or with that of fixation of the saccule and cochlear duct. Its intrinsic structure suggests that the cisternal septum is developed independently in chelonians, but the limited sampling precludes positivism concerning this point, and sheds little light on the structural or functional significance of the membrane.

The origin of the helicotrema is related to the cochlear duct in a manner similar to that noted in Rhynchocephalia and Squamata, and the relationships of the terminal part of the channel to the posterior acoustic foramen, to the cochlear ganglion and its branches, and to the limbus are similar to those found in representatives of the groups named. The intermediate part, on the other hand, diverges from the cochlear duct and shows a unique relationship to the medial wall of the saccule in its course toward the posterior acoustic foramen. It is interesting to note that an anteroventral "overgrowth" of the saccule, which penetrated between the helicotrema and anterior wall of the otic capsule in a form having a primitive labyrinthine organization, would produce changes in the helicotrema such as those noted; it would also produce altered relationships of the saccule, cochlear duct and lateral periotic structures to the lateral wall of the otic capsule. It seems reasonable to assume that such a development may have taken place early in the chelonian line, and resulted in the apparent rotation of intracapsular structures seen in modern turtles. Such an assumption seems entirely compatible with the mode of development and definitive structure of the otic capsule as described by de Beer (1937).

As in ophidians, the chelonian scala tympani is undoubtedly homologous to the scala of lacertilians, plus part of the periotic

sac. The origin of the channel shows relationships identical to those in Squamata, and the vertical expansion adjacent to the basilar membrane represents the intracapsular part of the periotic sac as it is seen in lacertilians. That part of the scala tympani posterior to the cochlear duct seems to represent that which, in lacertilians, would be the proximal (capsular) extremity of the extracapsular part of the periotic sac. This is borne out by the intracapsular relationship of the glossopharyngeal nerve to the scala, and finds support in the development of the posterior part of the capsule; de Beer (1937) points out that the internal and external glossopharyngeal foramina represent the medial and lateral apertures of the recessus scalae tympani, and indicates that the anterior extremity of the metotic fissure is incorporated into the otic capsule. The chelonian periotic sac is, therefore, the equivalent of only the posterior extremity of the extracapsular part of the rhynchocephalian or lacertilian periotic sac. Although the arrangement of the scala and periotic sac can be derived from a lacertilian type of organization, relationships to the vagus foramen and contained structures suggest that it probably arose by modification of parts little advanced from the presumed primitive organization resembling that in *Sphenodon*.

The paracapsular sinus (pericapsular sinus of de Burlet, 1934) shows consistent morphology in the forms included in this study, and is apparently like that which de Burlet (*ibid.*) describes in *Testudo*; no indication of an elaborate organization such as that author attributes to *Emys* is present, either in these forms or in the one late embryo of *Emys* I have examined. It seems clear that, as de Burlet suggests, the structure must function as a dampening or release mechanism for movements of the periotic fluid, and would thus be analogous to the juxtastapedial sinus of ophidians. On the other hand, the origin or derivation of the structure is enigmatic. Based solely upon the structure in adult animals, the paracapsular sinus could be derived by postulating extension of the periotic sac into relationship with the footplate (and cranial cavity, if the situation is as de Burlet describes it in adults of *Emys*), with a secondary separation of the extension from the parent cavity. This explanation finds no support in the development of the compartment in embryos of *Chrysemys*, for the periotic sac and paracapsular sinus appear independently and remain so in late (32mm.) embryos. A second possibility is that the paracapsular sinus may actually represent an isolated and highly modified superomedial part of the lining

of the tympanic cavity of an ancestral form. As noted above, the paracapsular sinus occupies a major part of the recessus cavi tympani, an area occupied by the tympanic cavity in most reptiles (Romer, 1956). The relationships of the sinus to the facial nerve and internal carotid artery seem to be compatible with such a suggestion, when viewed in the light of the osteological modifications which have occurred in the region. An additional feature of interest is the transverse communication between the right and left paracapsular sinuses noted in embryos of *Chrysemys*. The position of this communication is reminiscent of that of the intertympanic canals of crocodylians (van Beneden, 1882) and at least some mesosuchians (Edinger, 1938). I have found no reference to this channel in the literature, but Nick (1912) shows suggestions of its presence in several of his figures. Its developmental relationships to the pharyngeotympanic tube are not completely clear in the embryonic material available to me, but there is no doubt that both are, morphologically, intimately associated with the paracapsular sinus. Taken together, these items tend to support derivation of the sinus from a part of the lining of the tympanic cavity, but such a conclusion must be considered tentative until more detailed information concerning the development of the tympanic region in turtles is available.

Crocodylians, like chelonians, show major labyrinthine changes indicative of a long independent history. The most significant intracapsular changes influencing periotic channels are the altered positional relationships of the cochlear duct and the relatively tremendous elaboration of that structure. The lateral shift of the cochlear duct results in modified form of the periotic cistern, but its relationships to the lateral wall of the saccule and to the vestibular membrane are retained and the footplate of the columella auris impinges upon the periotic cistern opposite these surfaces. This differs from the situation de Burlet (1929) reports in *Crocodylus*, for he suggests that the footplate is directed only toward the vestibular membrane, and that the saccular part of the cistern is probably not significantly influenced by impulses introduced by the footplate.

The scala vestibuli, although elongated, extends along the distal part of the cochlear duct in relationship to the vestibular membrane and gives rise to a scala lagenae at its distal extremity; there seems to be no reason to question the direct homology of these channels to those given the same name in other reptiles. Conversely, the homology of the crocodylian helicotrema with that in other reptiles is open to question.

In all other reptiles examined, or adequately reported in the literature, the helicotrema is quite consistent in several features of its course and relationships. It turns medially around the antero-superior surface of the rostral extremity of the cochlear duct and passes medial to the lagenar and cochlear ramuli extending from the cochlear ganglion; furthermore, its relationship to the medial wall of the otic capsule inferior to the posterior acoustic foramen is inflexible. This course and relationships would be duplicated in crocodilians by a channel which arose from the medial aspect of the distal extremity of the scala vestibuli, entered the periotic tissue between the limbus and medial wall of the cochlear recess, and coursed proximally to terminate in the scala tympani opposite the posterior acoustic foramen posterior to the genu of the cochlear duct. The crocodilian helicotrema does not follow such a course, but passes directly from the scala vestibuli to the scala tympani around the lateral margin of the cochlear duct; this relationship would find its equivalent in a helicotrema which passed ventral to the cochlear duct in lacertilians. It is conceivable that this type of association is the result of a fundamental change in the relationships between the helicotrema and cochlear duct, but this seems unlikely in view of the consistency mentioned above. A second possibility, attractive because of its simplicity, would be that an adventitious communication between the two limbs of the helicotrema replaces the normal channel; such a process may have occurred, but it is probably more complex than indicated here.

Retzius (1884) describes and figures periotic spaces in the periotic tissue attaching the limbus to the medial wall of the cochlear recess. These spaces are clear in my material; in young specimens of *Alligator* and *Caiman*, they appear as a series of discontinuous small compartments irregularly aligned along the course postulated for a typical reptilian helicotrema. In late embryos of the same forms, the spaces are relatively larger and show more continuity than they do in older specimens, and in these embryos the helicotrema could not be clearly defined at the lateral margin of the limbus. Taken together, these items suggest that the series of periotic spaces in the medial limbic attachment represents remnants of a typical reptilian helicotrema. It follows that the definitive crocodilian helicotrema is, indeed, a secondary development, but could not have made communication with any part of the medial limb of the original helicotrema. It also indicates that the scala tympani of the distal limb of the cochlear duct is not the direct homolog

of the scala tympani of other reptiles, a fact that finds additional support in the manner in which the scala is "embraced" by the limbus. The presence of a definitive accessory scala tympani at the distal extremity of the basilar membrane suggests an explanation for the derivation of the scala tympani and for the crocodilian helicotrema as well.

Accepting the periotic spaces medial to the limbus as representative of the primitive channel (helicotrema) connecting the scala vestibuli with the periotic sac, contact of the periotic fluid with the basilar membrane of the distal limb of the cochlear duct must have been maintained by means of an accessory scala tympani which traversed the central part of the limbus. With extensive development, such a channel would have been separated from the lateral margin of the scala vestibuli by the more delicate of the limbic attachments, one which is less firm distally than proximally. Under these circumstances, an adventitious communication of the scala vestibuli with the distal part of the accessory scala tympani might easily have occurred at the lateral limbic attachment. Thus, the crocodilian scala tympani distal to the genu of the cochlear duct probably represents the greater part of a highly developed accessory scala tympani, only the tip of which remains recognizable as an entity.

The intracapsular part of the periotic sac requires special comment only in the sense that the part of the periotic system so designated has usually been included as part of the scala tympani (Retzius, 1884; de Burlet, 1929, 1934; and others). Although such nomenclature is undoubtedly justified on the basis of homology of the structure, the size of the channel plus its relationship to the periotic foramen differentiate it morphologically from the remainder of the scala tympani; it seems desirable to recognize this difference, together with the basic similarity in the relationships of the compartment to those in lacertilians, by the use of the term periotic sac. The latter term also serves to differentiate this part of the channel from the two accessory scalae and the derived scala tympani.

Retzius (1884) rather clearly describes the exit of the periotic sac (his "scala tympani") from the otic capsule by way of the periotic foramen (his "foramen recessus scalae tympani") in *Alligator*. It is clear from his description that he regards the space occupied by the extracapsular part of the periotic sac as the recessus scalae tympani. This is supported by de Beer's (1937) osteological analysis of *Crocodylus*, for he describes bony relationships similar

to those found in *Alligator* and *Caiman*, and elucidates the manner in which the processus subcapsularis extends the recessus scalae tympani laterally to form the fenestra pseudorotunda. A confusing note is introduced by de Beer (1937:263), however, for he states:

"The ductus perilymphaticus does not pass through the foramen perilymphaticum (de Burlet, 1929), and thus the 'recessus scalae tympani' in the crocodile fails to contain the scala tympani of the perilymphatic space. The restricted apertura lateralis of the 'recessus scalae tympani,' enclosed between the processus subcapsularis and the wall of the auditory capsule, and across which the secondary tympanic membrane is stretched, bears analogy (but *not* homology) to the mammalian fenestra rotunda, and may therefore in the crocodile be known as the fenestra pseudorotunda."

The apparent conflicts in these statements may be the result of confusion in terminology, but de Burlet (1929, 1934) does imply that the terminal part of the periotic system bears no relationship to the recessus scalae tympani, and de Beer fails to clarify the matter.

In both *Alligator* and *Caiman*, (and presumably in crocodiles since the bony relationships are so similar) the intracapsular part of the periotic sac communicates freely through the laterally-placed periotic foramen with the extracapsular part of the periotic sac. The latter is situated in the space between the processus subcapsularis and the lateral wall of the otic capsule, and contributes to the formation of the secondary tympanic membrane at the fenestra pseudorotunda. It seems obvious, as de Beer suggests, that the processus subcapsularis has extended the recessus scalae tympani laterally and superiorly to the area immediately posteroventral and lateral to the plane of the fenestra ovalis. The lateral placement of the periotic foramen results in the bulk of the extracapsular part of the periotic sac being situated lateral rather than posteroinferior to the otic capsule. The ventromedial extension of the sac into relationship with the glossopharyngeal and vagus nerves, and with the meninges, leaves no doubt concerning its homology. It seems probable that this extension indicates a more posteromedial placement of the extracapsular part of the sac in more primitive forms. The extension is certainly analogous (if not homologous) to the periotic duct of the cochlear aquaeduct of mammals, and the intimacy of its relationship to both the ninth and tenth nerves seems to preclude its derivation from any form in which a definitive recessus scalae tympani was present.

Although the middle ear has been considered extensively, features of the morphology of the internal ear have never been adequately evaluated in problems of reptilian taxonomy or phylogeny. Shute and Bellairs (1953) have described the highly-developed limbic

lip of geckos and pygopodids, and utilized this characteristic in suggesting affinities between these groups. In their introductory remarks they comment:

"Although the differences observed between the inner ears of various kinds of lizards may well have some relationship to their powers of hearing, it is seldom possible to explain them in terms of adaptive modification since they have no obvious association with the habits of the forms which exhibit them. In this respect the inner ear as a whole differs from both the middle ear and the eye, which are very subject to adaptive changes, particularly in lizards where their reduction is often associated with loss of the limbs and the assumption of burrowing habits. Observations on a relatively conservative structure such as the inner ear are therefore likely to have special significance in a consideration of the phylogenetic history and affinities of the groups studied."

Although these authors refer particularly to lizards, their comments seem, in light of the evidence of this investigation, to be applicable to the inner ear of reptiles in general. A fundamental conservatism in labyrinthine organization is evident in the major taxonomic assemblages, and there is no evidence of changes which are clearly degenerative in nature. It should be noted, however, that the inability to make "obvious association" of changes in the inner ear with the known habits of the forms showing them does not preclude the possibility of such modifications being adaptive; it is probable that they cannot be appreciated as such because of our limited information concerning reptilian auditory physiology and natural history. In the absence of such information, any attempt to interpret reptilian phylogeny and affinities on the basis of auditory structure must be conservative, but there are indications that studies of the morphology of the inner ear might well augment other lines of investigation.

The major changes in the anatomy of the periotic labyrinth correspond well with generally-accepted ideas of the interrelationships of the major assemblages of reptiles. Representatives of the Chelonia, Rhynchocephalia, Squamata and Crocodilia are clearly separable on the basis of major alterations in the organization of the labyrinth, and, within the Squamata, the ophidian periotic labyrinth appears to be a direct derivative of one similar to that in modern lacertilians. Only limited inferences can be drawn concerning the origins of these ordinal groups because of lack of adequate paleontological information concerning the osteology of the otic region in primitive reptiles. As noted above, it seems probable that the periotic labyrinth of *Sphenodon* is similar to that which must have been present in captorhinomorphs, forms referred to a position near reptilian "stem stock." The Lepidosauria show rela-

tively little intracapsular change from the presumed primitive pattern of the labyrinth, and the derivation of the extracapsular periotic relationships in the Squamata is simple and distinctive. Chelonians and crocodylians show divergent major intracapsular and extracapsular modifications of obvious antiquity; the morphology of the labyrinths of both lines can, however, be logically derived from the presumed primitive organization.

In the smaller taxonomic assemblages, several features seem worthy of note, but will require additional investigation to establish their general applicability. In those families of the Squamata represented in this study by more than one form, the periotic labyrinth (and otic labyrinth) tends to show a characteristic familial morphology. In some groups (*e. g.*, skinks and geckos) the identifying features are distinctive, while in others (*e. g.*, iguanids and lacertids) they are more subtle and involve labyrinthine relationships and proportions rather than special structures. Despite the common characteristics within families, however, differences between related genera are obvious, and there are indications that the morphology of the labyrinth is diagnostic to the level of the species. Within both the family and the genus the structures showing the greatest tendency to vary are those which are probably directly concerned with the transmission and reception of vibrations. These include the footplate, the periotic scalae and sac, the lagenar and saccular maculae, and the basilar papilla. Changes in these structures are so obvious in forms such as the skinks and geckos that they undoubtedly reflect some alteration in auditory function, but, as Shute and Bellairs (1953) observe, it is impossible to make direct correlations with the known habits of the animals showing the change.

Either positive or extensive comment on interfamilial relationships is precluded by the limited sample employed in this investigation, but some observations seem worthy of record. Intracapsular specialization in geckos is greater than indicated by Shute and Bellairs (*ibid.*) and involves both the otic and periotic labyrinths. The differences noted in labyrinthine organization in these forms tend to support Underwood's (1954) recognition of the families Eublepharidae, Sphaerodactylidae and Gekkonidae, but cast some doubt on the propriety of including *Aristelliger* in the family last named. Leptoglossan families show a series of common labyrinthine characteristics and show some evidence of progressive specialization within the infraorder. Indications of divergent progressive change in the periotic system are also found in the Iguanidae. On the

whole, the morphology of the lacertilian periotic labyrinth tends to indicate at least three lines of change which correspond to the assemblages given by Romer (1956) as the Iguania, Nyctisauria and Leptoglossa. On the other hand, the known otic morphology of forms included is that author's Diploglossa cannot be interpreted at this time.

In his reports, de Burlet (1929, 1934) indicates that *Anguis* shows characteristics of the periotic system which resemble those found in *Sphenodon*; notable among these is the passage of the periotic sac through part of the cranial cavity and its projection through the vagus foramen. Such an arrangement, differing radically from that in *Ophisaurus*, might be attributed to either retention of primitive features in the inner ear, or convergence associated with loss of the tympanic cavity. *Varanus*, the only other member of the infraorder in which the anatomy of the inner ear has been investigated in some detail, shows resemblances to *Ophisaurus*, but is unusual in that an accessory scala tympani is developed. These findings certainly seem to substantiate Romer's (1956) observation that, ". . . the group (Diploglossa) is a very diverse one, and its naturalness might be questioned." Furthermore, it seems probable that an intensive study of otic morphology might contribute significantly to clarification of the affinities which exist within the group.

In the absence of experimental studies dealing directly with the manner in which the periotic labyrinth functions in reptiles, two concepts are to be found either stated or implied in the literature dealing with the reptilian ear. One, quite positively stated by de Burlet (1934), holds that vibrations introduced into the periotic cistern by the footplate traverse the full length of the periotic channels, stimulate the basilar papilla as they pass in relationship to the basilar membrane, and are finally dampened at the peripheral extremity of the periotic sac. Conversely, Wever and Vernon (1956) unquestioningly assume that vibrations traverse the periotic cistern, cochlear duct and periotic sac in sequence, stimulating the basilar papilla in their passage through the duct. The same concept is implied by Shute and Bellairs (1953) when they state, ". . . the anterior half of the papilla basilaris lies in the direct line of fluid impulses transmitted across the perilymphatic cistern and cochlear duct from the footplate of the stapes." The second view conforms to current thinking concerning the mode of transmission of vibrations through the mammalian cochlea, and finds considerable support in Tonndorf's (1959) report of experiments

in which models (resembling the reptilian inner ear) were used to study the transfer of energy across the cochlea.

The morphological information accumulated here lends indirect support to the concept of direct transmission of energy through the inner ear in reptiles. In all forms other than crocodylians, the major part of the basilar papilla would be encompassed by lines projected from the margins of the footplate to the margins of the periotic foramen. In those forms in which the periotic foramen lies directly opposite the footplate, the peripheral attachments of the latter are of a nature that suggests a pistonlike movement in normal function; in those in which the foramen is not aligned with the footplate but (usually) posterior to it, one part (usually anterior) of the fibrous peripheral attachment is lax and suggests that the movement of the footplate would be of a "rocking" or "hinged" type. Both of these arrangements would result in the propagation of cisternal pressure waves in which the maximal displacement (and energy) would be directed toward the basilar papilla and periotic foramen. In no form does the vestibular membrane seem to be sufficiently thick to impede direct transmission of vibratory movement from the fluid of the periotic cistern to the otic fluid of the cochlear duct. On the strength of these relationships alone, a strong case can be made for vibrations introduced at the footplate traversing the periotic cistern, vestibular membrane and otic fluid of the cochlear duct, then distorting the tectorial membrane, basilar papilla and basilar membrane as they are transmitted toward the periotic sac and final dampening. Such reasoning does not, however, completely negate the possibility of transmission of vibrations along the circuitous route formed by the periotic channels. Such a concept does seem to be obviated by the relationships found in forms in which an accessory scala tympani is present. In these, vibrations carried along the full length of the periotic channels would conceivably reach those parts of the basilar membrane contacted by the accessory scala (assuming that decay in their original energy content had not rendered them valueless as a stimulus), but would find themselves "trapped" in the sense that no release or dampening route exists at the distal extremity of the accessory scala tympani; thus, all residual energy would necessarily be transferred through the basilar membrane into the otic fluid, a situation which seems entirely incompatible with efficient functioning of the fluid system. On the other hand, the accessory scala forms a logical and efficient pathway for the conduction of vibrations from the cochlear duct

to the dampening structures at the periphery of the periotic sac. These concepts are diagrammatically represented in Figures 53 and 54. It should be noted that, in those forms showing much elongation of the basilar papilla, pressure waves transmitted directly from the footplate to the periotic foramen would efficiently stimulate only that part of the papilla opposite the foramen; such relationships suggest that energy transfer may involve the formation of both pressure waves and traveling waves, and occur in a fashion similar to that elucidated by Tonndorf (1959). Invocation of such an explanation is particularly necessary in crocodylians.

The function of the reptilian basilar papilla as an auditory receptor is firmly established, but questions exist concerning the functions of the lagenar and saccular maculae. There is some agreement that the latter probably has a role in audition (de Burlet 1929, 1934; Weston, 1939), but expressed opinions concerning the function of the lagenar macula are rare. Weston (*ibid.*) attributes an auditory function to the receptor and suggests that it (together with the saccular macula) may operate in reception differing qualitatively from that of the basilar papilla. No suggestion is offered concerning a possible route for vibratory stimuli to reach the maculae, but tacit agreement with de Burlet (1934) is implied. The latter rules out the possibility of conduction of vibrations to the lagenar macula by the periotic fluid, and considers only the basilar papilla to be a periotic receptor (perilymphatische Sinnesendstelle) in reptiles.

In the forms utilized in this investigation, the lagenar part of the cochlear duct is, invariably, directly related to some part of the lateral body of periotic fluid (periotic cistern and/or its extensions); a similar situation exists in the case of the sacculae. The common relationship is one in which the periotic contact is made opposite the macula and its overlying otolith, usually at the thin lateral walls of the sacculae and cochlear duct. This relationship is in itself suggestive of a functional association between impulses propagated in the periotic fluid and the maculae. Additional support for such an interpretation is found in the extensions of the lateral fluid body developed in those forms in which direct relationship with the periotic cistern or scala vestibuli does not exist. The scala lagenae is a relatively constant feature, but is developed only to the extent required for full periotic relationship to the lagena. The scala sacculi, more striking in its departure from the usual periotic pattern, is best developed as a discrete channel in those forms in which

the normal lateral association of the saccule with the periotic cistern is lost. The variable morphology noted suggests that the channel may function differently in different forms; in practically all cases, however, it can be interpreted functionally only as a fluid pathway for the transmission of vibratory stimuli. I submit, therefore, that the saccular and lagenar maculae in reptiles not only subserve a function in the reception of vibratory stimuli, but that they are also periotic receptors. There is no question that their auditory function differs from that of the basilar papilla, since the otolithic mass associated with each would hardly be adapted to analysis of complex sounds; furthermore, this is not intended to suggest that audition is the sole macular function. Subjectively, it appears that the basilar papilla, the saccular macula and the lagenar macula constitute an auditory triad; the basilar papilla probably functions in analytical reception of sounds, and the maculae in non-analytical reception. The tendency of the three receptor areas to vary in size interdependently, as noted above and reported by Weston (1939), lends support to this interpretation. It would, indeed, be interesting to know if associations of the relative sizes of these receptors could be made with the habits and habitats of a variety of forms.

LITERATURE CITED

- BAST, T. H. and B. J. ANSON.
1949. The Temporal Bone and the Ear. Springfield: Thomas. pp. xviii + 478.
- DE BEER, G. R.
1929. The development of the skull of the shrew. *Phil. Trans. Roy. Soc. Lond. (B)*, vol. 217, pp. 411-480.
1937. The Development of the Vertebrate Skull. Oxford. pp. xxiii + 552.
- VAN BENEDEEN, E.
1882. Recherches sur l'orielle moyenne des Crocodiliens et ces communications multiples avec le pharynx. *Arch. Biol.*, vol. 3, pp. 497-560.
- BENSLEY, R. R., and S. H. BENSLEY.
1938. Handbook of Histological and Cytological Technique. Chicago: University of Chicago Press. pp. viii + 167.
- DE BURLET, H. M.
1929. Zur vergleichenden Anatomie und Physiologie des perilymphatischen Raumes. *Acta Oto-laryng. Stockh.*, vol. 13, pp. 153-187.
1934. Vergleichende Anatomie des stato-akustischen Organs. a. Die innere Ohrsphäre. b. Die mittlere Ohrsphäre. In *Handbuch der vergleichenden Anatomie der Wirbeltiere*, vol. 2, pp. 1293-1432. Ed. Bolk *et al.* Berlin und Wien: Urban & Schwarzenberg.
- CLASON, E.
1871. Die Morphologie des Gehörorgans der Eidechsen. *Anat. Studien*, herausg. v. C. Hasse, vol. 2, Leipzig.

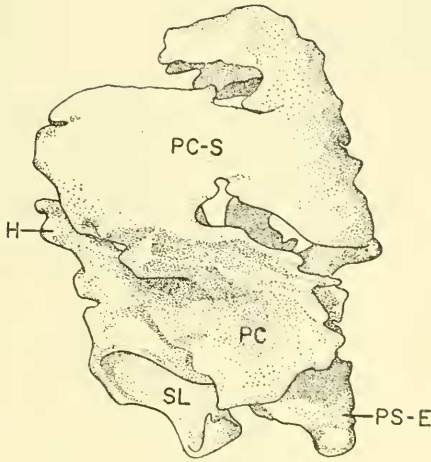
- EDINGER, T.
1938. Ueber Steinkerne von Hirn- und Ohr-höhlen der Mesosuchier *Goniopholis* und *Pholidosaurus* aus dem Bückelburger Wealden. *Acta Zool. Stockh.*, vol. 19, pp. 467-505.
- VON FRISCH, K.
1938. The sense of hearing in fish. *Nature, Lond.*, vol. 141, pp. 8-11.
- GAUPP, E.
1900. Das Chondrocranium von *Lacerta agilis*. *Anat. Hefte, Arb.*, vol. 15, pp. 433-595.
- GRAY, P.
1954. *The Microtomist's Formulary and Guide*. Philadelphia: Blakiston. pp. xiii + 794.
- GRAY, O.
1955. A brief survey of the phylogenesis of the labyrinth. *Jour. Laryng. and Otol.*, vol. 69, pp. 151-179.
- HAAS, G.
1930. Ueber das Kopfskelett und die Kaumuskulatur der Typhlopiden und Glauconiiden. *Zool. Jahrb., Abt. Anat.*, vol. 52, pp. 1-94.
- HARRISON, H.
1902. On the perilymphatic spaces of the amphibian ear. *Internat. Monatschr. f. Anat. u. Phys.*, vol. 19, pp. 221-261.
- HASSE, C.
1873a. Die vergleichende Morphologie und Histologie des häutigen Gehörorgans der Wirbelthiere. *Suppl. z. d. Anat. Studien*, herausg. v. C. Hasse, vol. 1. Leipzig.
1873b. Die Lymphbahnen des inneren Ohres der Wirbelthiere. *Anat. Studien*, herausg. v. C. Hasse, vol. 4. Leipzig.
- MÖLLER, W.
1905. Zur Kenntnis der Entwicklung der Gehörknöchelchens bei der Kreuzotter und der Ringelnatter nebst Bemerkungen zur Neurologie dieser Schlangen. *Arch. Mikr. Anat.*, vol. 65, pp. 439-497.
- NICK, L.
1912. Das Kopfskelet von *Dermochelys coriacea* L. *Zool. Jahrb., Abt. Anat.*, vol. 33, pp. 1-238.
- OELRICH, T. M.
1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Misc. Publ. Mus. Zool., Univ. Mich.*, no. 94, pp. 1-122.
- OSAWA, G.
1898. Beiträge zur Lehre von den sinnesorganen der *Hatteria punctata*. *Arch. Mikr. Anat.*, vol. 51, pp. 481-691.
- PRICE, L. I.
1935. Notes on the brain case of *Captorhinus*. *Proc. Boston Soc. Nat. Hist.*, vol. 40, pp. 377-385.
- RETZIUS, G.
1881. Das Gehörorgan der Wirbelthiere. I-Das Gehörorgan der Fische und Amphibien. Stockholm. pp. xi + 222.
1884. Das Gehörorgan der Wirbelthiere. II-Das Gehörorgan der Reptilien, der Vögel und der Säugethiere. Stockholm. pp. viii + 368.

- RICE, E. L.
1920. The development of the skull in the skink, *Eumeces quinquelineatus*; I-the chondrocranium. Jour. Morph., vol. 34, pp. 119-243.
- ROMER, A. S.
1956. Osteology of the Reptiles. Chicago: University of Chicago Press. pp. xxi + 772.
- SHUTE, C. C. D., and A. D' A. BELLAIRS
1953. The cochlear apparatus of Geckonidae and Pygopodidae and its bearing on the affinities of these groups of lizards. Proc. Zool. Soc. Lond., vol. 123, pp. 695-709.
- SMITH, H. M.
1946. Handbook of Lizards. Ithaca: Comstock, pp. xxi + 557.
- STREETER, G. L.
1918. The histogenesis and growth of the otic capsule and its contained periotic tissue-spaces in the human embryo. Carnegie Contrib. Embr., vol. 7, pp. 5-54.
- TONNDORF, J.
1959. The transfer of energy across the cochlea. Air University, School of Aviation Med., 59-49, pp. 1-11.
- UNDERWOOD, G.
1954. On the classification and evolution of geckoes. Proc. Zool. Soc. Lond., vol. 124, pp. 469-492.
- WALTNER, J. G.
1948. Barrier membrane of the cochlear aqueduct. Arch. Otolaryng., vol. 47, pp. 656-669.
- WESTON, J. K.
1939. Notes on the comparative anatomy of the sensory areas of the vertebrate inner ear. Jour. Comp. Neuro., vol. 70, pp. 355-394.
- WEVER, E. G. and J. A. VERNON
1956. Sound transmission in the turtle's ear. Proc. Nat. Acad. Sci., vol. 42, pp. 292-299.
- WOLFF, D., R. J. BELLUCCI and A. A. EGGSTON
1957. Microscopic Anatomy of the Temporal Bone. Baltimore: Williams & Wilkins. pp. viii + 414.
- WYETH, F. J.
1924. The development of the auditory apparatus in *Sphenodon punctatus*. Phil. Trans. Roy. Soc. Lond. (B), vol. 212, pp. 259-368.
- YOUNG, M. W.
1952. The termination of the perilymphatic duct. Anat. Rec., vol. 112, pp. 102-103.

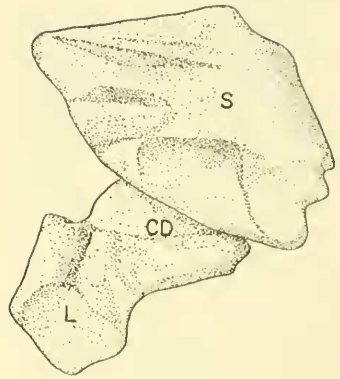
KEY TO ABBREVIATIONS

- AOA—anterior otic ampulla
ASD—anterior semicircular duct
AST—accessory scala tympani
BP—basilar papilla
CD—cochlear duct
CS—cisternal septum
DR—ductus reuniens
FP—footplate of columella auris
H—helicotrema
JS—juxtastapedial sinus
L—lagena
Lb—limbus
LOA—lateral otic ampulla
LSD—lateral semicircular duct
MC—meningeal contact of periotic sac at medial
aperture of the recessus scalae tympani
MI.—macula lagenae
MS—macula sacculi
OC—otic capsule
OD—otic duct
PC—periotic cistern
PC-S—saccular part of periotic cistern
PCS—paracapsular sinus
PF—periotic foramen
POA—posterior otic ampulla
PS—periotic sac
PS-I—intracapsular part of periotic sac
PS-E—extracapsular part of periotic sac
PSD—posterior semicircular duct
S—sacculi
SCP—subcapsular process
SL—scala lagenae
SS—scala sacculi
ST—scala tympani
STM—secondary tympanic membrane
SV—scala vestibuli
U—utricle
USD—utricle-sacculi duct
VIII—acoustic nerve
IX—glossopharyngeal nerve
X—vagus nerve

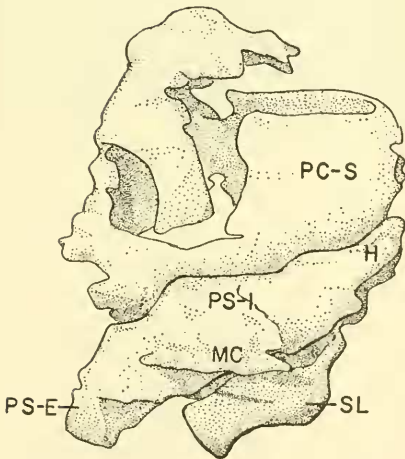
FIGURES 3-6



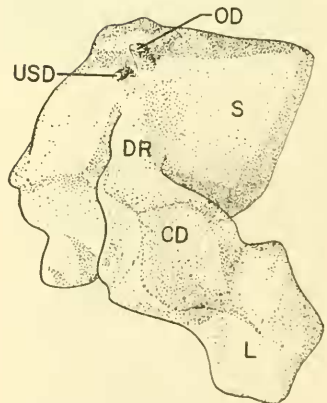
3.



4.



5.



6.

Reconstructions of the Inferior Divisions of the Labyrinths of *Sphenodon*

FIG. 3. Lateral view of the left periotic labyrinth of a late embryo. 29X

FIG. 4. Lateral view of the left saccule and cochlear duct of a late embryo. 29X

FIG. 5. Medial view of the left periotic labyrinth of a late embryo. 29X

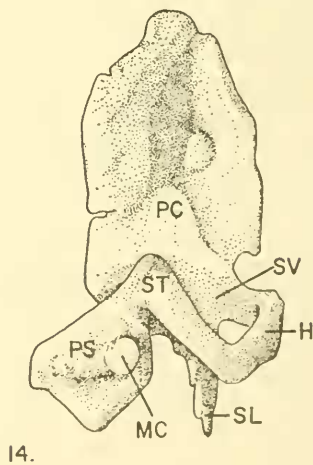
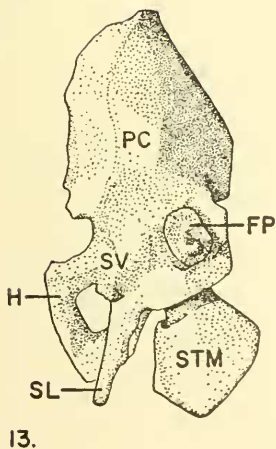
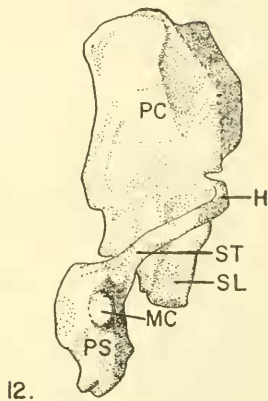
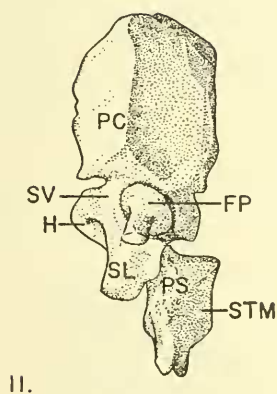
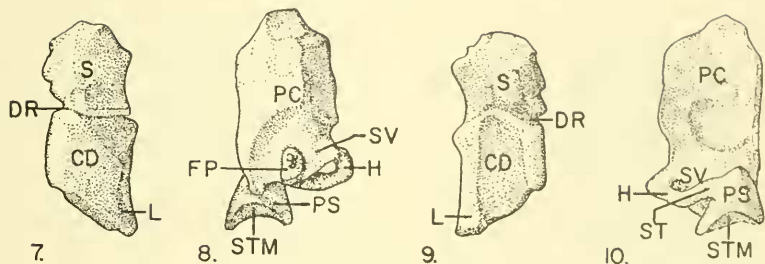
FIG. 6. Medial view of the left saccule and cochlear duct of a late embryo. 29X

FIGURES 7-14

Reconstructions of the Inferior Divisions of the Labyrinths of Iguanid Lizards

- FIG. 7. Lateral view of the right saccule and cochlear duct of *Anolis*. 17×
FIG. 8. Lateral view of the right periotic labyrinth of *Anolis*. 17×
FIG. 9. Medial view of the right saccule and cochlear duct of *Anolis*. 17×
FIG. 10. Medial view of the right periotic labyrinth of *Anolis*. 17×
FIG. 11. Lateral view of the left periotic labyrinth of *Phrynosoma*. 17×
FIG. 12. Medial view of the left periotic labyrinth of *Phrynosoma*. 17×
FIG. 13. Lateral view of the left periotic labyrinth of *Crotaphytus*. 17×
FIG. 14. Medial view of the left periotic labyrinth of *Crotaphytus*. 17×

FIGURES 7-14



FIGURES 15-20

Reconstructions of the Inferior Divisions of the Labyrinths of Gekkonoid
Lizards

FIG. 15. Lateral view of the left periotic labyrinth of *Coleonyx*. 22×

FIG. 16. Medial view of the left periotic labyrinth of *Coleonyx*. 22×

FIG. 17. Medial view of the left sacculle and cochlear duct of a late embryo of *Aristelliger*. 25×

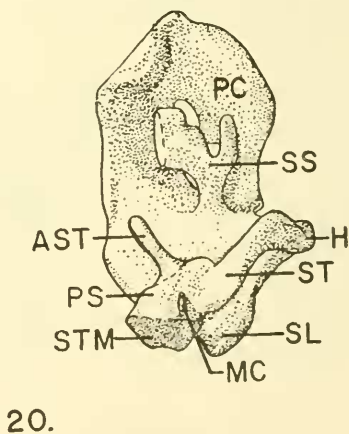
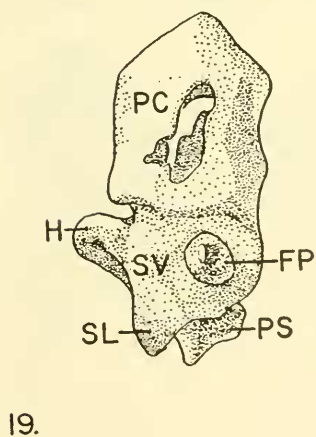
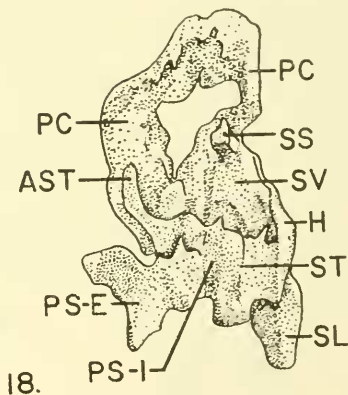
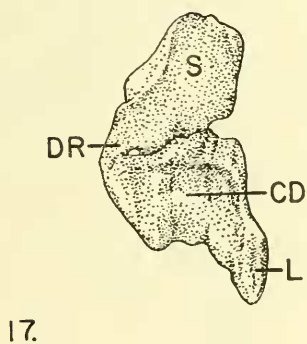
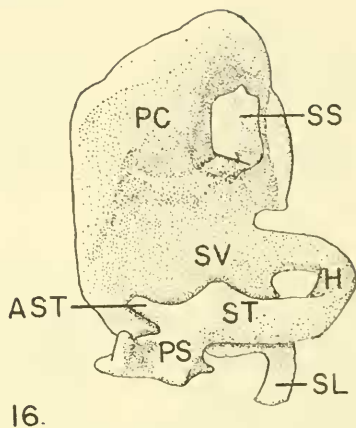
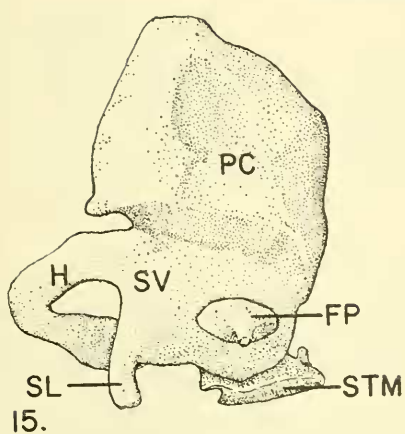
FIG. 18. Medial view of the left periotic labyrinth of a late embryo of *Aristelliger*. 25×

Note opening in periotic cistern resulting from laterally expanded sacculle, and the incomplete development of the scala sacculi.

FIG. 19. Lateral view of the left periotic labyrinth of *Hemidactylus*. 22×

FIG. 20. Medial view of the left periotic labyrinth of *Hemidactylus*. 22×

FIGURES 15-20



FIGURES 21-31

Reconstructions of the Inferior Divisions of the Labyrinths of Leptoglossans

FIG. 21. Lateral view of the left periotic labyrinth of *Cnemidophorus*. 14×

FIG. 22. Medial view of the left saccule and cochlear duct of *Cnemidophorus*. 14×

FIG. 23. Medial view of the left periotic labyrinth of *Cnemidophorus*. 14×

FIG. 24. Lateral view of the left periotic labyrinth of *Eumeces obsoletus*. 14×

FIG. 25. Medial view of the left saccule and cochlear duct of *E. obsoletus*. 14×

FIG. 26. Medial view of the left periotic labyrinth of *E. obsoletus*. 14×

FIG. 27. Lateral view of the left periotic labyrinth of *Eumeces fasciatus*. 14×

FIG. 28. Medial view of the left periotic labyrinth of *E. fasciatus*. 14×

Note obvious differences of parts from those in *E. obsoletus*.

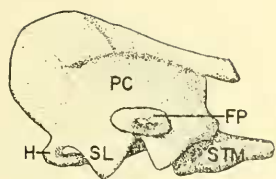
FIG. 29. Lateral view of the left periotic labyrinth of a late embryo of *Lacerta*. 22×

FIG. 30. Medial view of the left saccule and cochlear duct of a late embryo of *Lacerta*. 22×

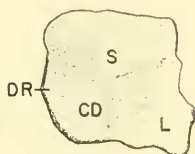
FIG. 31. Medial view of the left periotic labyrinth of a late embryo of *Lacerta*. 22×

Note development of saccular part of the periotic cistern and absence of a scala sacculi at this stage.

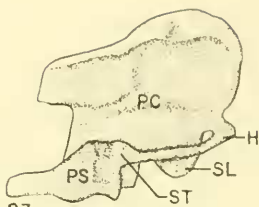
FIGURES 21-31



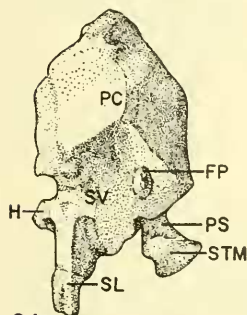
21.



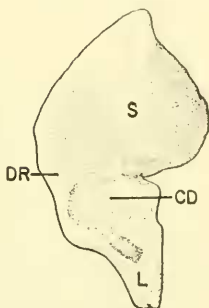
22.



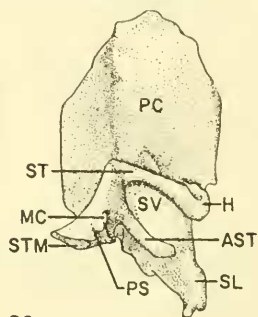
23.



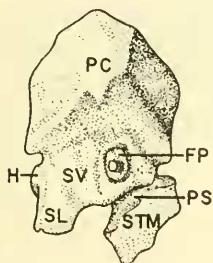
24.



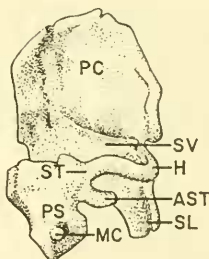
25.



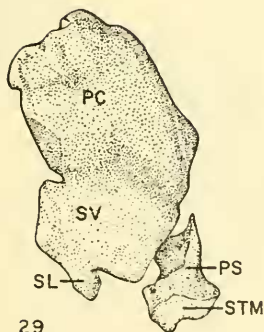
26.



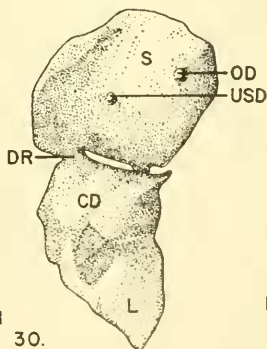
27.



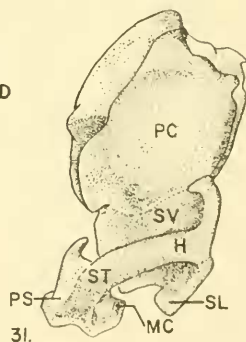
28.



29.



30.



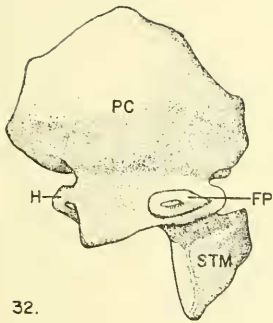
31.

FIGURES 32-37

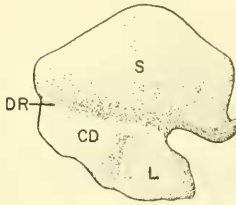
Reconstructions of the Inferior Divisions of the Labyrinths of Diploglossans

- FIG. 32. Lateral view of the left periotic labyrinth of *Ophisaurus*. 13×
- FIG. 33. Medial view of the left saccule and cochlear duct of *Ophisaurus*.
13×
- FIG. 34. Medial view of the left periotic labyrinth of *Ophisaurus*. 13×
- FIG. 35. Medial view of the left saccule and cochlear duct of *Varanus*.
13×
- FIG. 36. Lateral view of the left periotic labyrinth of *Varanus*. 13×
- FIG. 37. Medial view of the left periotic labyrinth of *Varanus*. 13×

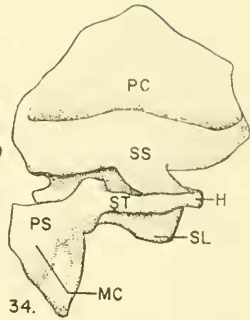
FIGURES 32-37



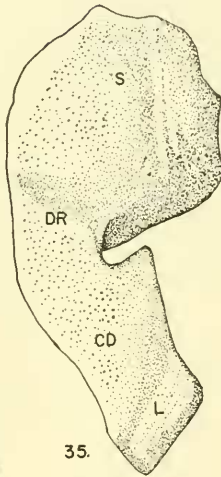
32.



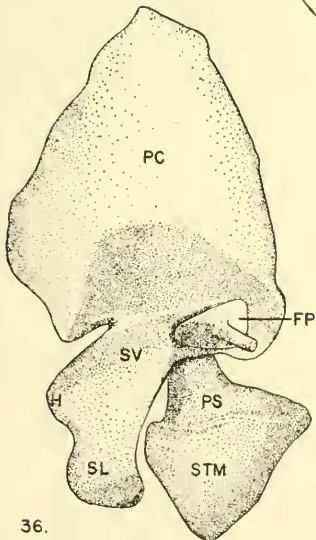
33.



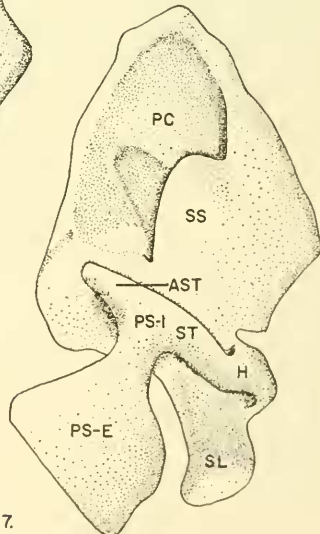
34.



35.



36.



37.

FIGURES 38-41

Some Auditory Structures of Colubrid Snakes

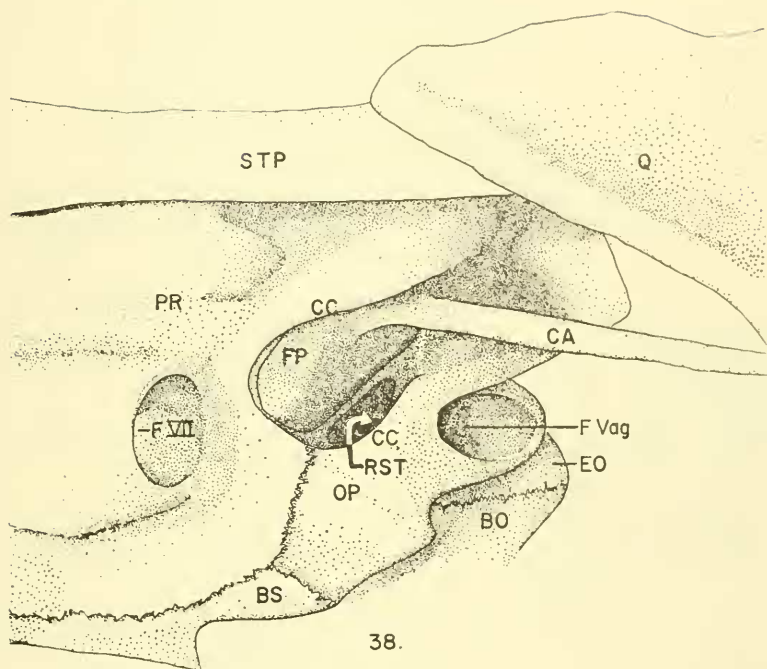
Fig. 38. Lateral view of the left otic region in a skull of *Thamnophis*. 23 × BO-basioccipital; BS-basisphenoid; CA-columella auris; CC-circumfenestral crest; EO-exoccipital; FVag-vagus foramen; FVII-foramen of facial nerve (part); OP-opisthotic; PR-prootic; Q-quadrata; RST-recessus scalae tympani; STP-supratemporal; FP-footplate. Note the juxtastapedial fossa (unlabeled) delimited by the circumfenestral crest.

Fig. 39. Medial view of a reconstruction of the left sacculle and cochlear duct of *Diadophis*. 33 ×

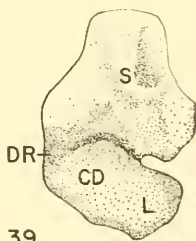
Fig. 40. Lateral view of a reconstruction of the inferior division of the left periotic labyrinth of *Diadophis*. 33 ×

Fig. 41. Medial view of a reconstruction of the inferior division of the left periotic labyrinth of *Diadophis*. 33 ×

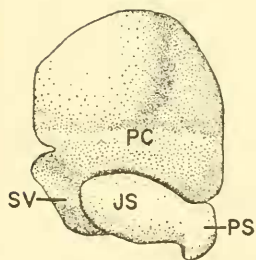
FIGURES 38-41



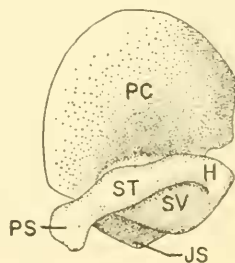
38.



39.



40.



41.

FIGURES 42-45

Reconstructions of the Inferior Divisions of the Labyrinths and Paracapsular Sinus of *Chrysemys*

Fig. 42. Lateral view of the left saccule and cochlear duct of a late embryo. 40×

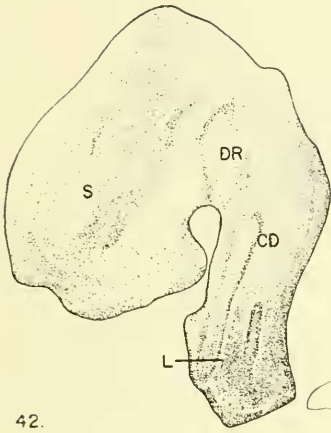
Fig. 43. Lateral view of the inferior division of the left periotic labyrinth of a late embryo. 40×

Outline of paracapsular sinus shows its relationship to periotic structures, and the base of the canal (arrow) which connects right and left sinuses in the embryo.

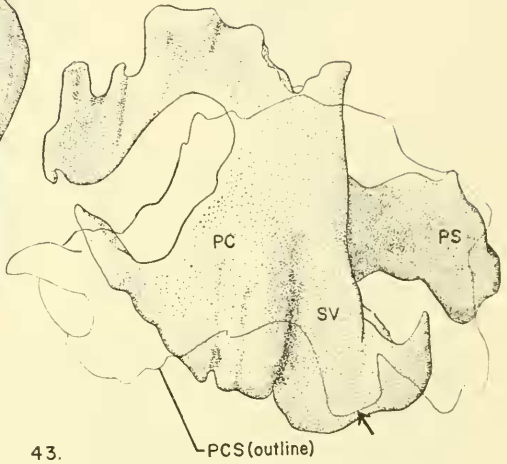
Fig. 44. Medial view of the left saccule and cochlear duct of a late embryo. 40×

Fig. 45. Medial view of the inferior division of the left periotic labyrinth and paracapsular sinus of a late embryo. 40×

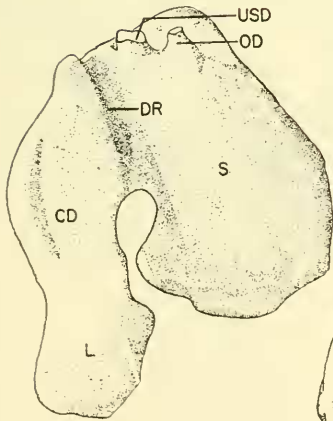
FIGURES 42-45



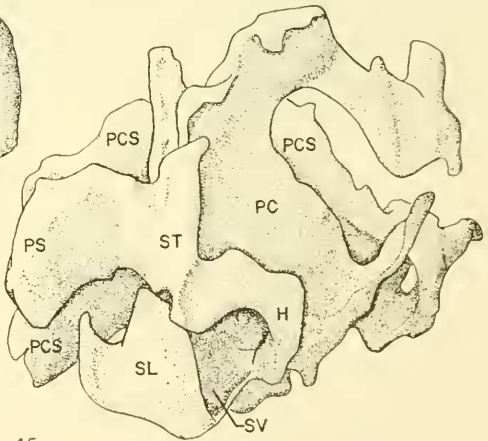
42.



43.



44.



45.

FIGURES 46-54

Schematic Representations of the Internal Ear in Several Reptiles

FIG. 46. Lateral view into the inner ear of a crocodylid; footplate and periotic foramen are superimposed to show relationships.

Note small accessory scala tympani (unlabeled) invading limbus at each extremity of the basilar membrane.

FIG. 47. Transverse section through the footplate and periotic foramen in a crocodylid.

Note free extension of periotic sac through periotic foramen into the recessus scalae tympani.

FIG. 48. Frontal section through the inner ear of *Sphenodon*.

FIG. 49. Frontal section through the inner ear of a chelonian.

FIG. 50. Frontal section through the inner ear of a colubrid snake.

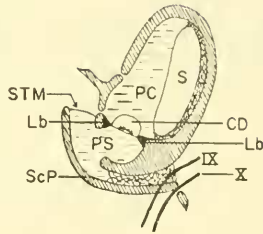
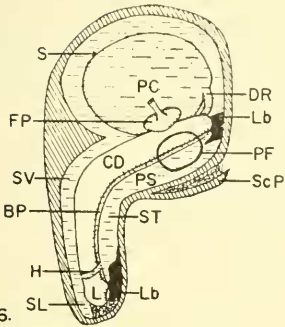
FIG. 51. Transverse section through the inner ear of a lacertilian in which the secondary tympanic membrane is situated deep in the recessus scalae tympani.

FIG. 52. Transverse section through the inner ear of a lacertilian in which the periotic sac fills the recessus scalae tympani.

FIG. 53. Frontal section through the inner ear of a scincid illustrating transmission of energy according to the concept cited by de Burlet (1934). Note "trapping" of energy in accessory scala tympani.

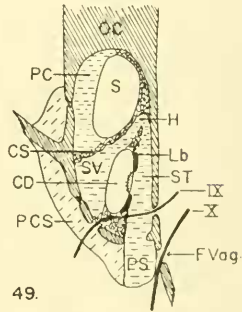
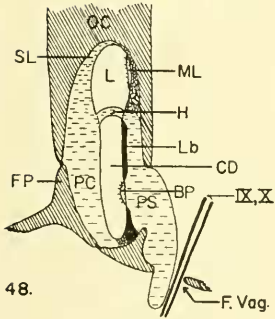
FIG. 54. Frontal section through the inner ear of a scincid illustrating the concept of direct transmission of energy.

FIGURES 46-54



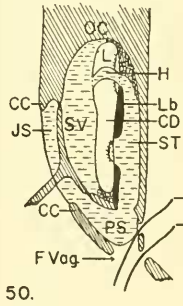
46.

47.

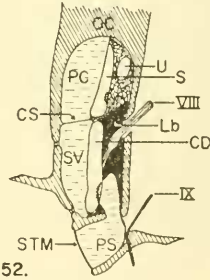


48.

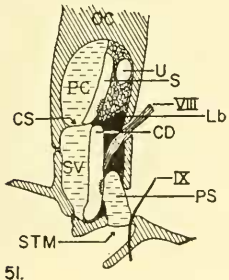
49.



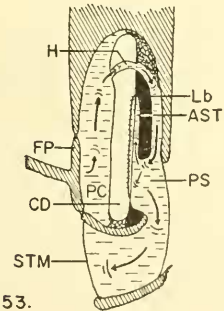
50.



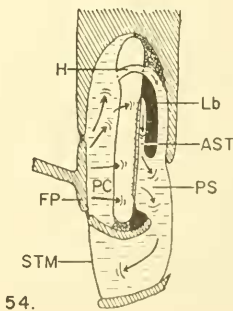
52.



51.



53.



54.